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THE DEVELOPMENT OF SOCIAL COGNITION DURING ADOLESCENCE

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ABSTRACT

This thesis aims to investigate the development of social cognition during adolescence. Neuroimaging research has provided new evidence for significant developments of the brain during adolescence, contesting old notions that the human brain reaches maturity by childhood. The prefrontal, parietal and superior temporal cortices have been highlighted as the regions that undergo the most prolonged and profound structural change. Given the association of these brain areas with social cognitive tasks, including perspective taking, intention understanding and motor imagery, this series of studies have sought to investigate the social cognitive consequences of these brain developments.

The first study in this thesis investigated the development of perspective taking between late childhood and adulthood and found that perspective taking develops in terms of efficiency and possibly strategy during adolescence. The second study investigated perspective taking in adult patients with positive symptoms of schizophrenia, including delusions of persecution, and suggested differences in processing one's own and other people's perspectives in patients compared to normal controls. The third study used fMRI to investigate the development of the neural circuitry for intentional causality during adolescence and found a shift from relatively higher activity in superior temporal cortex during adolescence to relatively higher activity in medial prefrontal cortex in adulthood. In light of motor theories of social cognition, the fourth study comprised three motor imagery experiments that investigated the development of action representation during adolescence. Results suggested that the action representation system is refined during adolescence. The final study compared action representation in typically developing adolescents and those with autism spectrum disorders and found no differences in performance between groups.

Together, these studies have shown that certain social cognitive abilities develop during adolescence. The relation between social and motor cognition is discussed from a developmental perspective, as well as the link to brain maturation during adolescence. Finally speculations are made about how these processes may become dysfunctional in psychopathology.

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GLOSSARY

Brain imaging techniques
EEG: electroencephalography
fMRI: functional magnetic resonance imaging
MEG: magnetoencephalography
MRI: magnetic resonance imaging
PET: positron emission tomography
TMS: transcranial magnetic stimulation

Brain areas
ACC: anterior cingulate cortex
AI: anterior insula
DLPFC: dorsolateral prefrontal cortex
FC: frontal cortex
IFG: inferior frontal gyrus
IPL: inferior parietal lobe
MPFC: medial prefrontal cortex
OFC: orbitofrontal cortex
PC: parietal cortex
PFC: prefrontal cortex
STS: superior temporal sulcus
TPJ: temporo-parietal junction
VPMC: ventral premotor cortex

Neural matter
GM: grey matter
WM: white matter
MN: mirror neuron

Functions and systems
TOM: theory of mind
MNS: mirror neuron system

Groups
TD: typically developing
ASD: autism spectrum disorder
DCD: developmental coordination disorder
NC: normal control adults
P-: patients with affective disorders but no/minimal positive symptoms
P+: patients with positive symptoms of schizophrenia

Experimental tasks and conditions
1PP: first-person perspective
3PP: third-person perspective
O: open
C: closed
IC: intentional causality
PC: physical causality
VGPT: visually guided pointing task

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THE DEVELOPMENT OF THE ADOLESCENT BRAIN AND COGNITION

CHAPTER 1

1. INTRODUCTION

1.1. Adolescence: psychological, social and physical transitions

Adolescence is a transitional time between childhood and adulthood, characterized by major hormonal and physical changes and developments in identity, self-consciousness and cognitive flexibility (Coleman & Hendry, 1990; Feldman & Elliott, 1990; Rutter, 1993). Social relationships seem to be of particular importance during adolescence. There seems to be a qualitative shift in the nature of thinking such that adolescents are more self-reflective and conscious of others than prepubescent children (Steinberg, 2005). Adolescents also develop a capacity to hold in mind more multidimensional concepts and are thus able to think in a more strategic manner (Petersen, 1988). New research in social cognitive neuroscience has begun to suggest that the adolescent brain may be adaptive to the behaviourally demanding social environment during this period. Empirical research on cognitive and neural development during puberty and adolescence is in its initial stages. In the past few years, several pioneering experiments have investigated the development of brain and cognitive processes during this period of life. Even though brain adaptation can occur throughout the lifespan, the maturational phases during early life, that is, during fetal development, childhood and adolescence are thought to be the most dramatic (Toga et al., 2006). The first section of this introduction begins by outlining the cellular studies that first demonstrated anatomical brain developments during adolescence. It then goes on to describe how recent brain imaging techniques have supported these findings and have shed some light on the trajectories of maturational processes in the brain during adolescence. The sections that follow discuss investigations of cognitive development, in particular, studies of executive functions using behavioural and functional imaging techniques. The second section of this introduction discusses theories of intersubjectivity from a social cognitive neuroscience perspective.

1.2. Evidence for the development of the adolescent brain

1.2.1. The first experiments on adolescent brains

Until recently, very little was known about brain development during adolescence. The notion that the brain continues to develop after childhood is relatively new. Experiments on animals, starting in the 1950s, showed that sensory regions of the brain go through 'critical periods' or 'sensitive periods' soon after birth, during which time environmental stimulation appears to be crucial for normal brain development and for normal perceptual development to occur (e.g. Hubel & Wiesel, 1962) These experiments on the development of the animal visual cortex suggested that there is a 'critical period' in which an alteration in the normal pattern of activity during a time window in early life dramatically alters cortical inputs and responses, whereas a similar alteration later in life has no obvious effect. These experiments suggested the human brain might be susceptible to the same sensitive periods in early development, that is, a period of susceptibility to the effects of a certain type of stimulus.

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It was not until the late 1970s that research on post-mortem human brains revealed that some brain areas continue to develop well beyond early childhood, which in turn suggested that sensitive periods for the human brain may be more protracted than previously thought. It was shown that cellular events take different trajectories in different areas of the human brain (Huttenlocher, 1979). Synaptic density in the visual cortex reaches a peak during the fourth postnatal month, and is followed by the elimination of synapses and the stabilisation of synaptic density to adult levels before the age of four. On the other hand, the structure of the prefrontal cortex (PFC) undergoes significant changes during puberty and adolescence (Huttenlocher, 1979; Huttenlocher et al., 1983; Yakovlev & Lecours, 1967). Two main changes were revealed in the brain before and after puberty. As neurons develop, a layer of myelin is formed around their extension, or axon, from supporting 'glial' cells. Myelin acts as an insulator and massively increases the speed of transmission (up to 100 fold) of electrical impulses from neuron to neuron. Whereas sensory and motor brain regions become fully myelinated in the first few years of life, although the volume of brain tissue remains stable, axons in the frontal cortex (FC) continue to be myelinated well into adolescence (Yakovlev & Lecours, 1967). The implication of this research is that the

transmission speed of neural information in the FC should increase throughout childhood and adolescence.

The second difference in the brains of pre-pubescent children and adolescents pertains to changes in synaptic density in the PFC. An adult brain has about 100 billion neurons; at birth the brain has only slightly fewer neurons (Pakkenberg & Gundersen, 1997). However, during development many changes take place in the brain. Neurons grow, which accounts for some of the change, but the wiring, the intricate network of connections -- or synapses -- between neurons, sees the most significant change. Early in postnatal development, the brain begins to form new synapses, so that the synaptic density (the number of synapses per unit volume of brain tissue) greatly exceeds adult levels. This process of synaptic proliferation, called synaptogenesis, lasts up to several months, depending on the species of animal and brain region. At this point, synaptic densities in most brain regions are at their maximum. These early peaks in synaptic density are followed by a period of synaptic elimination (or pruning) in which frequently used connections are strengthened and infrequently used connections are eliminated. This experience-dependent process, which occurs over a period of years, reduces the overall synaptic density to adult levels.

These data came mainly from studies of sensory regions of animal brains. The first demonstration of synaptogenesis was in 1975, when it was found that in the cat visual system the number of synapses per neuron first increases rapidly and then gradually decreases to mature levels (Cragg, 1975). Further research carried out in rhesus monkeys (Rakic, 1995) demonstrated that synaptic densities reach maximal levels two to four months after birth, after which time pruning begins. Synaptic densities gradually decline to adult levels at around three years, around the time monkeys reach sexual maturity.

However, synaptogenesis and synaptic pruning in the *prefrontal cortex* has a rather different time course. Histological studies of monkey and human PFC have shown that there is a proliferation of synapses in the subgranular layers of the PFC during childhood and again at puberty, followed by a plateau phase and a subsequent elimination and reorganisation of prefrontal synaptic connections after puberty (Bourgeois et al., 1994; Huttenlocher, 1979; Woo et al., 1997; Zecevic & Rakic, 2001).

According to these data, in the human brain, synaptic pruning occurs throughout adolescence and results in a net decrease in synaptic density in the medial PFC (MPFC) during this time. The focus of this chapter will be on cognitive implications of this second wave of synaptogenesis in PFC at the onset of puberty and the process of synaptic pruning that follows it after puberty.

Synaptic pruning is believed to be involved in the fine-tuning of functional networks of brain tissue, rendering the remaining synaptic circuits more efficient. Synaptic pruning is thought to underlie sound categorisation, for example. Language learning typically occurs immediately after birth, and requires picking out the meaningful sound distinctions from the continuous speech stream infants are exposed to. Babies are born with the ability to distinguish between many more speech contrasts than occur in their own language. However, by the end of their first year of life, they appear to lose the ability to distinguish between sounds which do not signal meaningful linguistic differences (see Kuhl, 2004 for review). For example, before about 12 months of age babies brought up in the USA can detect the difference between certain sounds common in the Hindi language, which after 12 months they can no longer distinguish (Werker et al., 1981). In contrast, babies brought up hearing the Hindi language at the same age remain sensitive to these distinctions. Based on these experiments, the idea that the human brain may continue to undergo substantial change after early sensitive periods seemed unlikely.

However, more recent research has questioned this view of brain plasticity. Kuhl has recently proposed a model of Native Language Neural Commitment (NLNC) in which experience-driven language learning produces dedicated neural networks that code the patterns of spoken language (statistical and prosodic patterns). If one is only exposed to one native language, the system will 'settle', or become committed to this, and subsequent violations (e.g. hearing a foreign language) will not be processed optimally. There is evidence that the systems of infants brought up bilingually 'settle' later (Kuhl, 2004) and experience in later life can still influence and change these networks (e.g. second language learning; Teaching the /r/-/l/ discrimination to Japanese adults (McClelland et al., 2002)). Thus the idea of a 'sensitive period' has become less rigid and typified by the significant neural changes that take place when experience-driven learning is occurring. Many skills like language have to be learnt early, but it is thought

that other significant skills can only be learnt later, for example, complex social cognition, perhaps because there are certain aspects about adult social relationships that an infant can not learn in a socially 'dependent' role (J. Thomson, personal comm.). Although there is no direct evidence linking the cellular brain changes with sound processing, this fine-tuning of sound categorisation is thought to rely on the pruning of synapses in sensory areas involved in processing sound. The studies on post-mortem brain development suggest that development of cognitive processes associated with the frontal lobes may well continue throughout adolescence.

1.2.2. Viewing the adolescent brain with MRI

Until recently, the structure of the human brain could be studied only after death. The scarcity of post-mortem child and adolescent brains meant that knowledge of the adolescent brain was extremely scanty. Nowadays, non-invasive brain imaging techniques, particularly Magnetic Resonance Imaging (MRI), can produce detailed three-dimensional images of the living human brain (see Figure. 1.1). Since the advent of MRI, a number of brain imaging studies have provided further evidence of the ongoing maturation of the cortex into adolescence and even into adulthood.

1.2.2.1. Linear increases in white matter during adolescence

Since the first *in vivo* studies reflecting that in spite of somewhat larger total brain volumes, adults have less grey matter (GM) than children (Jernigan & Tallal, 1990), in the past few years, several MRI studies have been performed to investigate the development of the structure of the brain during childhood and adolescence in humans (cf. Casey et al., 2005; Paus, 2005). One of the most consistent findings from these MRI studies is that there is a steady increase in white matter (WM) in certain brain regions during childhood and adolescence. In one MRI study, a group of children whose average age was nine years, and a group of adolescents whose average age was 14, were scanned (Sowell et al., 1999). This study revealed differences in the density of white and GM between the brains at the two age groups. The results showed a higher volume of WM in the FC and parietal cortex (PC) in the older children than in the younger group. The younger group, by contrast, had a higher volume of GM in the same regions. Myelin appears white in MRI scans, and therefore the increase in WM and decrease in GM with age was interpreted as reflecting increased axonal myelination in the frontal

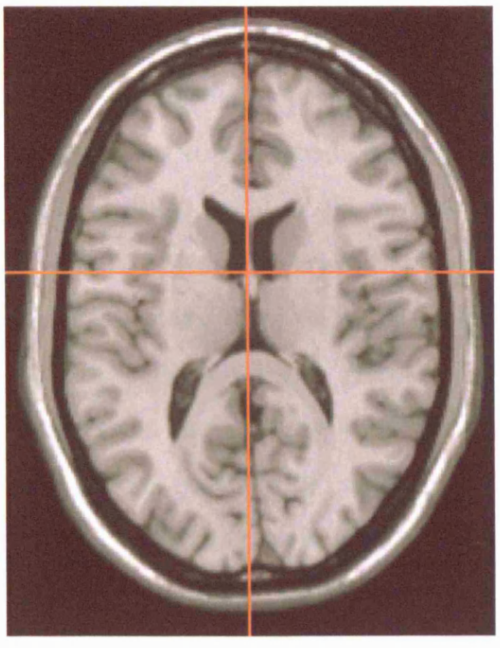

Figure 1.1. ***Magnetic Resonance Imaging (MRI)*** *uses a very large magnetic field to produce high-quality three-dimensional images of brain structures without injecting radioactive tracers. A large cylindrical magnet creates a magnetic field around the participant's head, and a magnetic pulse is sent through the magnetic field. The MRI signal is based on the magnetic properties of the protons within the nucleus of atoms. The signal depends on a property of the atoms called spin. When placed in a magnetic field, a spin has a magnetic moment. The net magnetic moment of all the spins in the magnetic field is the magnetisation vector and the majority of the spins in the magnetisation vector are aligned with the magnetic field. In order to observe a MRI signal the total magnetisation vector must be tipped away from the main field direction, to create a component of magnetisation precessing (rotating) about this axis, in the transverse plane. This is accomplished by exciting the spins by applying a radiofrequency magnetic field (the rf pulse) perpendicular to the main magnetic field. This changes the alignment of the proton magnetic moments so the spins are tipped away from their equilibrium position. As a result of this excitation the spins produce a rf signal - this is the MRI signal. Although tissue and fat contribute to the MR signal, the largest contributions come from the protons in tissue water. The image intensity is dependent on the density of these protons, and can also be affected by the local environment of the water molecules.*

and parietal cortices during this time period.

The increased WM and decreased GM density in FC and PC throughout adolescence has now been demonstrated by several studies carried out by a number of different research groups with increasingly large groups of participants (Giedd et al., 1996; 1999a; Pfefferbaum et al., 1994; Reiss et al., 1996; Sowell et al., 1999). Different studies point to developmental changes in WM density in different brain regions. Paus et al., (1999a) analysed the brain images of 111 children and adolescents aged between four and 17 years, and noted an increase in WM specifically in the right internal capsule and left arcuate fasciculus. The left arcuate fasciculus contains WM tracts that connect anterior speech regions (Broca's area) and posterior language regions (Wernicke's area). Thus the increase in WM in this region was interpreted as reflecting increased connections between the speech regions. The corpus callosum, the dense mass of fibres that connects the two hemispheres of the brain, has also been found to undergo region-specific growth during adolescence and up until the mid-twenties (Barnea-Goraly et al., 2005; Giedd et al., 1999b; Pujol et al., 1993).

While structural neuroimaging studies diverge in terms of the precise brain regions in which WM density increases have been found, they generally agree on the pattern of WM change. Most studies point to a steady, more-or-less linear increase in WM with age (Barnea-Goraly et al., 2005; Giedd et al., 1999a; Paus et al., 1999a; 1999b; Pfefferbaum et al., 1994; Reiss et al., 1996) and in light of histological studies (Yakovlev & Lecours, 1967) showing increasing levels of myelin in the human brain, WM increases in MRI (believed to signifiy myelinated tissue) have been interpreted to reflect continued axonal myelination during childhood and adolescence (see Figure 1.2A).

1.2.2.2. Non-linear decreases in grey matter during adolescence

While the increase in WM in certain brain regions seems to be linear across all brain areas, the changes in GM density appear to follow a region-specific, non-linear pattern. In other words, while WM development follows a steady, progressive course, GM development is at certain stages progressive and at other times regressive. As the following studies have shown, its pattern of development in certain brain regions follows an inverted-U shape (see Figure 1.2B).

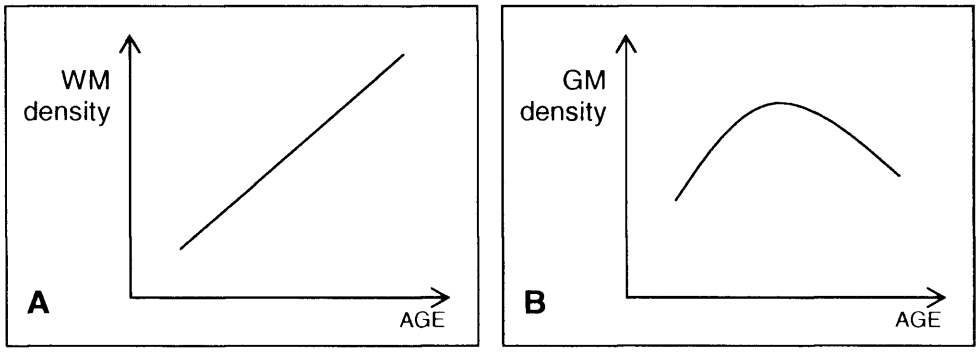

Figure 1.2. *WM and GM development with age.* ***A:*** *Linear development of WM with increasing age. This is thought to reflect a linear increase in myelination around axons.* ***B:*** *Non-linear development of GM. This is thought to reflect synaptogenesis followed by synaptic pruning.*

Giedd et al. (1999a) performed a longitudinal MRI study on 145 healthy boys and girls ranging in age from about four to 22 years. At least one scan was obtained from each of 145 participants (89 were male). Scans were acquired at two-year intervals for 65 of these participants who had at least two scans, 30 who had at least three scans, two who had at least four scans and one who had five scans. Individual growth patterns revealed heterochronous GM development during adolescence. Changes in the frontal and parietal regions were similarly pronounced. The volume of GM in the frontal lobe increased during pre-adolescence with a peak occurring at around 12 years for males and 11 years for females. This was followed by a decline during post-adolescence. Similarly, parietal-lobe GM volume increased during the pre-adolescent stage to a peak at around 12 years for males and 10 years for females, and this was followed by decline during post-adolescence. GM development in the temporal lobes was also non-linear, but the peak was reached later at about 17 years. While FC and PC development is relatively rapid during adolescence, GM in the superior temporal cortex, including superior temporal sulcus (STS), steadily declines during adolescence and across the lifetime, following an inverted U-curve and reaching maturity relatively late (Gogtay et al., 2004; Toga et al., 2006; see Figure 1.3). In the occipital lobes, GM development had a linear course.

A further MRI study of 35 normally developing children (7-11 years), adolescents (12-16 years) and young adults (23-30 years) demonstrated a sharp acceleration in the loss of GM between childhood and adolescence in the dorsal PFC and the dorsal PC (Sowell et al., 2001). In the frontal lobes, the decrease in GM density was even more pronounced between adolescence and adulthood. In addition, an inverse relationship between dorsal PFC growth and GM density was found to exist between childhood and adolescence. The regions exhibiting the most robust decrease in GM density also exhibited the most robust post-pubescent increase in WM density in the dorsal PFC.

In a longitudinal study of participants aged between four and 21, Gogtay et al., (2004) scanned 13 children every two years for eight to10 years. The authors suggested that phylogenetically older cortical areas mature earlier than the newer cortical regions. In the frontal lobe, maturation was shown to occur in a back-to-front direction, starting in the primary motor cortex (the precentral gyrus), then extending anteriorly over the superior and inferior frontal gyri.

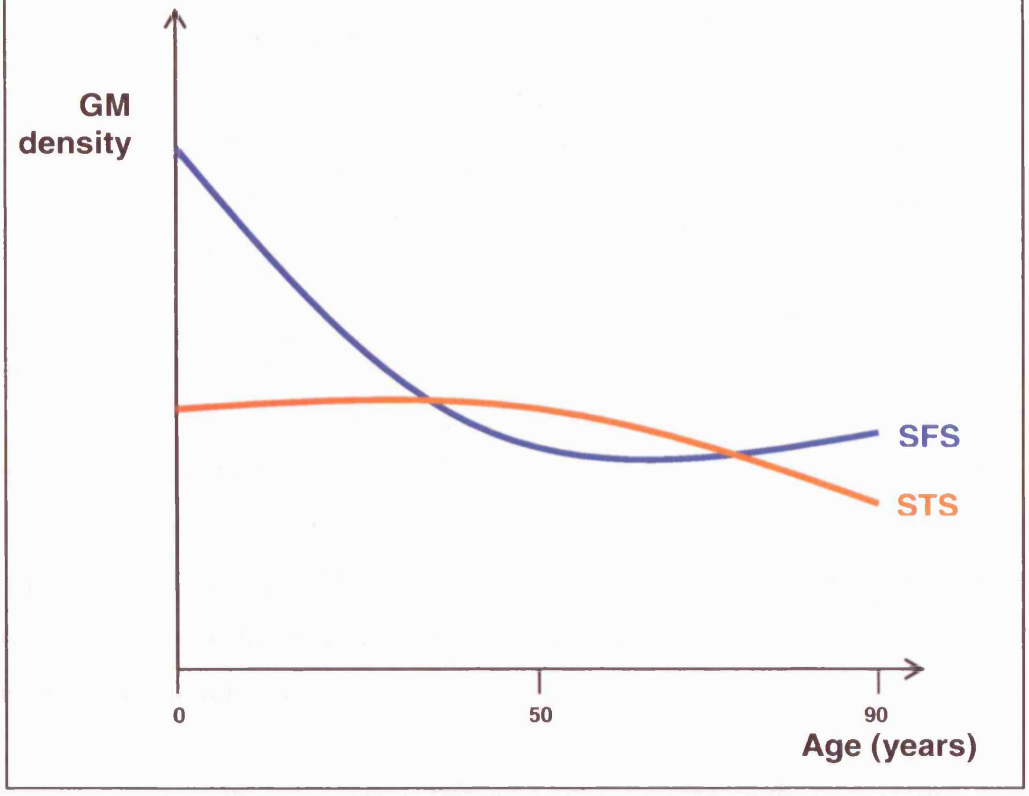

Figure 1.3. ***Grey matter density loss in superior frontal sulcus (SFS) and superior temporal sulcus (STS).*** *GM loss is rapid during adolescence in SFS while it follows a steadier and more prolonged course of development in STS (adapted from Toga et al., 2006).*

The PFC was shown to develop last. In the posterior half of the brain, the maturation began in the primary sensory area, spreading laterally over the rest of the parietal lobe. Lateral temporal lobes were the last to mature. The authors noted that the temporal lobes have a distinct maturation pattern. While the temporal poles matured early, other areas including superior temporal gyrus and STS matured latest in the brain. It was suggested that the sequence of structural maturation corresponds to the regionally relevant milestones in cognitive development. In other words, those brain areas associated with more basic cognitive skills, such as motor and sensory functions matured first, followed by brain areas (including PC) linked to spatial orientation and attention and finally the regions related to executive function (PFC).

A similar pattern of development was found in a longitudinal study of children aged from three to 15 years (Thompson et al., 2000). In this experiment, high spatial resolution maps of the brain's growth patterns were obtained using tensor mapping, with the same subject being scanned across time spans of up to four years. In the older group (11 to 15 years) a localized GM decrease in the FC was observed. This study provided further evidence of a sharp acceleration of GM density loss between childhood and adolescence in dorsal FC.

In summary, rather than a simple linear change in GM with age, studies suggest perturbation in GM density development that more or less coincides with the onset of puberty. At puberty, GM volume in the frontal lobe reaches a peak, followed by a plateau after puberty and then a decline throughout adolescence continuing until early adulthood. The MRI results demonstrating a non-linear decrease in GM in various brain regions throughout adolescence have been interpreted in two ways. First, it is likely that axonal myelination results in an increase in WM and a simultaneous decrease in GM as viewed by MRI. A second, additional explanation is that the GM changes reflect the synaptic reorganisation that occurs at the onset of and after puberty (Huttenlocher, 1979). Thus, the increase in GM apparent at the onset of puberty (Giedd et al., 1999a) might reflect a wave of synapse proliferation at this time. The gradual decrease in GM density that occurs after puberty in certain brain regions has been attributed to post-pubescent synaptic pruning (Giedd et al., 1999a; Gogtay et al., 2004; Sowell et al., 2001). In other words, the increase in GM at puberty has been interpreted to reflect a sudden increase in the number of synapses. At some point after puberty, there is a

process of refinement such that these excess synapses are eliminated (Huttenlocher, 1979). It is speculated that this synaptic pruning is reflected by a steady decline in GM density seen in MRI.

1.2.3. Gender differences in development of brain structure

Given that maturational rates and hormonal events differ between males and females, neuronal and cognitive differences might also be expected. Studies of rats as well as humans demonstrate that it is not just fluctuations of hormones but also anatomical differences that contribute to differences in cognition and behaviour. Aside from structural dimorphism of the hypothalamus, women also have larger hippocampi than men, when corrected for total brain size (Goldstein et al., 2001) and men have larger amygdalae than females (Cooke & Woolley, 2005; Goldstein et al., 2001), both of which are associated with differential cognitive capacities (Killgore et al., 2001; Kilpatrick et al., 2006; Maguire et al., 1999). The PFC is rich in sex hormones, with the highest concentration of oestrogen receptors in the brain (Bixo et al., 1995). Coupled with its structural development during adolescence, cognitive differences between the sexes might be expected during this period. Indeed, a cross-sectional MRI study of 46 children and adults (mean age 11) revealed significant differences in grey and WM between girls and boys, particularly in the inferior frontal gyrus (IFG) (Blanton et al., 2004). A significant age-related increase in WM volume in the left IFG was found in boys but no significant volumetric changes in girls in any frontal regions. Furthermore, even after correcting for total cerebral volume, boys had significantly greater GM volume in the IFG relative to girls. The authors speculated that these structural differences may arise from the difference in steroid levels between girls and boys, during pubertal maturation. It was suggested that the effect of inhibition of synaptic pruning from testosterone may account for greater volume in boys that in girls. On the other hand, it was proposed that greater hemispheric specialisation (Shaywitz et al., 1995) among boys may account for the gender differences in structure. So far, structural studies are not in full agreement with regard to gender differences. For example, in a longitudinal study, it was found that boys had 10% greater total cortical GM volume than girls, but that developmental trajectories of grey and WM volume were not significantly different (Giedd et al., 1999a). Larger longitudinal studies will help to overcome variability in FC anatomy, to discern gender differences more clearly.

1.2.4. Brain changes continue after adolescence

Recent MRI studies indicate that the time at which the brain reaches maturity may be much later than the end of adolescence. One study of participants aged between seven and 30 revealed that the loss of GM in the dorsal FC accelerated during adulthood between the early 20s and up to the age of 30 (Sowell et al., 2001).

A further MRI study by the same group involved scanning 176 individuals between seven and 87 years (Sowell et al., 2003). The results revealed a reduction in GM density in the dorsal prefrontal, dorsal parietal and posterior temporal cortices, which was accompanied by an increase in WM. The pattern of GM changes was non-linear during the period of adolescence. Although the decrease in GM was most dramatic from childhood to young adulthood, this study revealed that WM volume continued to increase well beyond this stage and even up to the age of 60. The non-linear decrease in GM was concomitant with a linear increase in WM, consistent with earlier MRI data and with post-mortem studies.

To summarise, in vivo MRI studies coupled with post-mortem cellular studies of human brains have revealed an extended period of development, in particular in the frontal, parietal and superior temporal cortices. Taken together, the studies provide consistent evidence for the dynamic nature of the adolescent brain with respect to maturational changes of grey and WM. The main changes that have been observed are a non-linear reduction in GM density and a simultaneous linear increase in WM.

1.3. Changes in behaviour and cognition after puberty

Two of the brain regions that have consistently been shown to undergo continued development during adolescence are PFC and PC. Given the continued developmental changes in these brain regions during adolescence, it might be expected that cognitive abilities that rely on the functioning of these regions and their complex interconnectivity with other regions, should also change during this time period. Most studies to date have investigated cognitive abilities subserved by the frontal lobes, in particular executive function.

1.3.1. The development of executive function

1.3.1.1. Behavioural studies of inhibitory control, working memory, decision-making and prospective memory

Most studies investigating cognitive development during adolescence have focussed on the frontal lobes. The term *executive function* is used to describe the capacity that allows us to control and coordinate our thoughts and behaviour (Luria, 1966; Shallice, 1982). These skills include selective attention, decision-making, voluntary response inhibition and working memory. Each of these executive functions has a role in cognitive control, for example filtering out unimportant information, holding in mind a plan to carry out in the future and inhibiting impulses. Much work on human and monkey brain and behaviour has associated these strategic behaviour skills with the frontal lobes. Lesion studies (Goldman-Rakic, 1987; Rakic et al., 1994; Shallice, 1982) and functional imaging experiments (e.g. Casey et al., 1997; Rubia et al., 2001; 2003) suggest that such skills rely heavily on the frontal lobes. Since MRI studies have demonstrated changes in FC during adolescence, executive function abilities might be expected to improve during this time. For example, selective attention, decision-making and response inhibition skills along with the ability to carry out multiple tasks at once, might improve during adolescence. Many studies have investigated the development of executive function skills in early and late childhood (e.g. Brocki & Bohlin, 2004; Casey et al., 1997; Klenberg et al., 2001; Paus, 1989; Paus et al., 1990). A few studies have investigated the changes in executive function skills during adolescence, the findings of which will be discussed in the following section.

Behavioural studies of performance of adolescents on tasks including inhibitory control (Leon-Carrion et al., 2004; Luna et al., 2004a), processing speed (Luna et al., 2004a), working memory and decision-making (Hooper et al., 2004; Luciana et al., 2005) continue to develop during adolescence (Luna et al., 2004a). Luna et al., for example, showed that performance on an oculomotor task undergoes a large improvement from childhood to adolescence, followed by a plateau between adolescence and early adulthood (Luna et al., 2004a). Another study investigating performance on a variety of executive function tasks between the ages of 11 and 17 demonstrated a *linear* improvement in performance on some tasks but not others (Andersen et al., 2001).

Tasks that showed improvement during adolescence included tasks of selective attention, working memory and problem solving, whereas strategic behaviour, as tested by the Tower of London task (Shallice, 1982), seemed to have been formed earlier in childhood. Different aspects of executive function, therefore, may have different developmental trajectories. These studies speculate that the developments found are linked to the pruning and myelination processes occurring during adolescence in the PFC. Given that these cognitive functions have been associated with PFC function, and that histological and MRI studies have shown ongoing structural maturation during the adolescent period, it is thought that executive function development may be supported by neural maturation in PFC (cf. Blakemore & Choudhury, 2006a).

Prospective memory is the ability to hold in mind an intention to carry out an action at a future time (Ellis, 1996), for example, remembering to make a phone call at specific future time. Prospective memory is associated with frontal lobe activity (Burgess et al., 2000) and has been shown to develop through childhood as we develop our future oriented thought and action (Ellis & Kvavilashvili, 2000). Multitasking is believed to be a test of prospective memory as it requires participants to remember to perform a number of different tasks, mirroring everyday life. In a recent study of the development of prospective memory from childhood to adulthood, a multitask paradigm was used to test children aged between six and 14 and adults (Mackinlay et al., 2003). Participants were scored for both efficiency and the strategies used to effectively carry out the task. A significant improvement in both the efficiency and quality of strategies was found between the age of six and ten. However, between the ages of 10 and 14, there was no significant change in performance. The adult group (mean age 25), on the other hand, significantly out-performed the children. The authors therefore suggested that prospective memory continues to develop during adolescence, in line with the notion of frontal maturation in the brain. It is possible that the lack of improvement in performance between the 10 and 14-year olds was related to their pubertal status. In other words, changes in the brain at puberty might affect cognitive function.

A *non-linear* pattern of development was found in a recent behavioural study that used a match-to-sample task (McGivern et al., 2002). In this task, volunteers were shown pictures of faces showing particular emotional expressions (happy, sad, angry), or words describing those emotions ("Happy," "Sad," Angry"), and were asked to specify,

as quickly as possible, the emotion presented in the face or word. In a third condition, volunteers were shown both a face and a word and had to decide whether the facial expression matched the emotional word. The rationale behind the design of the task was that the face/word condition places high demands on frontal lobe circuitry, since it requires working memory and decision-making. The task was given to a large group of children aged 10 to 17 years and a group of young adults aged 18 to 22 years.

The results revealed that, at the age of puberty onset, at 11-12 years, there was a decline in performance in the matching face and word condition compared with the younger group of children. A 10-20% increase in reaction time on the match-to-sample task occurred at the onset of puberty in the 10-11 year old group of girls and in the 11-12 year old group in boys, compared to the previous year group of each sex (age 9-10 and 10-11 in girls and boys, respectively). The results suggest that there is a dip in performance on this kind of task at the onset of puberty. After puberty, from age 13-14, performance improved until it returned to the pre-pubescent level by the age of about 16-17 years.

The researchers linked this pubertal dip in performance to the proliferation of synapses that occurs at the onset of puberty, followed by synaptic pruning and strengthening after puberty. Based on these behavioural results, and in the context of structural MRI studies discussed above, it was suggested that until pruning occurs after puberty, synaptic connections in the FC generate a low signal to noise ratio due to an excess of synapses, which renders the cognitive performance less efficient. So, the sudden proliferation of synapses at puberty results in a perturbation of cognitive performance. Only later, after puberty, are the excess synapses pruned into specialized, efficient networks, which are then thought to render cognitive function more efficient.

1.3.1.2. Viewing the adolescent brain in action with fMRI: neuroimaging studies of inhibitory control, generativity, risk assessment and learning

Functional MRI (fMRI) provides us with a safe, non-invasive tool to study interactions between brain and behaviour (see Figure 1.4). fMRI has been used only in a handful of studies investigating the neural bases of cognitive development using tasks designed to tap specifically into PFC function, in particular executive function tasks.

For example, through fMRI studies, the development of response inhibition, and the neural structures supporting it, has been well studied. A popular paradigm for studying inhibition is the Go/No-Go task, which involves inhibiting a response when a certain stimulus is shown. In one fMRI study that employed a version of this task , a group of children (seven-12 years old) and young adults (21-24 years old) were presented with a series of alphabetic letters and were required to press a button upon seeing each one, except when the letter X appears (Casey et al., 1997). Volunteers were instructed to refrain from pressing any buttons if they saw the letter 'X' – the No-Go stimulus. This task requires executive action: the command to inhibit a habitual response.

The results showed that in both children and adults, several regions in the FC, including the anterior cingulate, orbitofrontal cortex (OFC) and inferior and middle frontal gyri, were activated during the task that required inhibiting the normal response. While the location of activation was essentially the same for both age groups, there was a significantly higher volume of prefrontal activation in children than in adults, specifically in the dorsolateral PFC (DLPFC) and extending into the cingulate. By contrast, adults showed more activity in the ventral region of the PFC. Thus the activation in the DLPFC could be negatively correlated with behavioural performance (as interpreted from error rates), as distinct from the OFC whose activation increased with improvement in behavioural performance. In line with this pattern, those participants who performed best (that is, those who had lowest error rates) and had the greatest orbitofrontal activation, also had the least DLPFC activation. The greater and more diffuse activity in the dorsal region of the PFC in children suggests that there is a heavier dependence on this region in children compared with in adults. The researchers suggested that during adolescence, the network recruited for this task is modified until adulthood, at which stage activation of a smaller, more focal region of the PFC is used to perform the same task.

To substantiate speculations about brain activation during inhibition during the transition between childhood and adulthood, the study was replicated with a wider age range of participants (Tamm et al., 2002). In the second study, the same Go/NoGo task was used but participants included children as well as adolescents – this time, participants ranged in age from eight to 20 years old. While there was no difference in accuracy on the task with age, reaction times successfully to inhibit responses

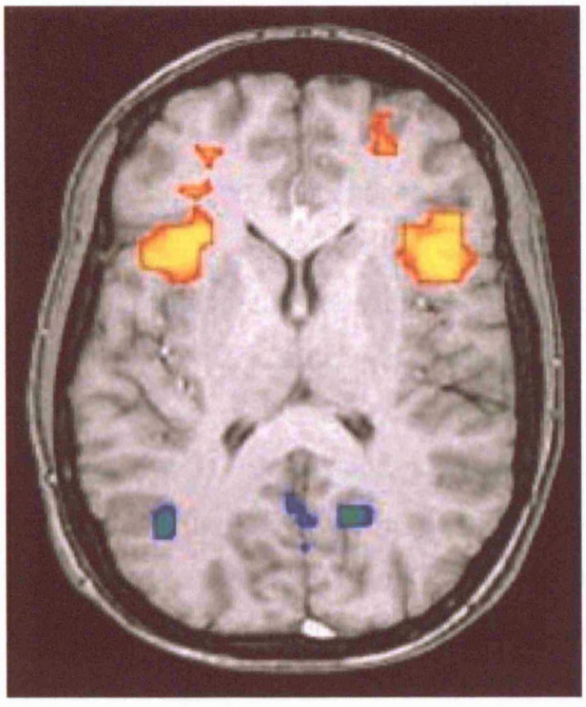

Figure. 1.4. ***Functional MRI (fMRI).*** *In the past 15 years, techniques have been developed that enable scientists to use MRI to image the brain at work. This is known as fMRI. When neurons become active they require a supply of oxygen to be carried to them in the blood. It is this oxygen carried in the blood that the fMRI scanner detects because of the magnetic properties of oxygen.*

Oxygen transport in the blood is mediated by haemoglobin, contained within red blood cells. The binding of oxygen to haemoglobin is regulated by local oxygen pressure: when the pressure is high oxygen is bound to haemoglobin; when the pressure is low oxygen is released. When haemoglobin has no oxygen bound to it, it has a net magnetic moment. As soon as oxygen becomes bound this, net moment disappears. Haemoglobin's paramagnetic behaviour thus depends on the amount of oxygen bound to it. The magnetic state of blood therefore reflects its level of oxygenation, with deoxyhaemaglobin being more paramagnetic than oxyhaemaglobin.

Because deoxyhaemaglobin is more paramagnetic than oxyhaemaglobin, a change in the MRI signal extending around the blood vessels can be caused by manipulating the oxygenation state of the blood. The more paramagnetic an agent the faster its relaxation time is, and the less signal it will produce. Therefore, deoxyhaemaglobin produces less MRI signal than oxyhaemaglobin. fMRI measures the amount of oxygenated blood that is sent to particular regions in the brain. This information is used to make 'films' of changes in brain activity as volunteers see or hear certain stimuli or perform other tasks, like answer questions tapping specific cognitive processes. Scanning a subject while he or she is performing a particular cognitive task should lead to activity changes in, and only in, the region of interest.

significantly decreased with age. fMRI data revealed age related increases in activation in the left inferior frontal gyrus extending to the OFC and, consistent with Casey et al.'s results, age related decreases in activation in both the left superior and middle frontal gyrus extending to the cingulate. These results demonstrated a dissociation between prefrontal areas in the development of inhibitory control and a negative correlation between age and brain activation.

This pattern of age-dependent activation has been corroborated by fMRI studies of generativity. Word generation tasks, for example, have been extensively used in experimental and clinical studies and are consistently linked to PFC activation and are therefore useful to study development of generativity in adolescence (Brown et al., 2005, Gaillard et al., 2000). A study using a verbal fluency task required children (average age 11 years) and adults (average age 29 years) to generate different words starting with the same letter as quickly as possible in the scanner (Gaillard et al., 2000). The results of this study revealed that children performed worse on the task and had on average 60% greater activation in the left inferior FC and the DLPFC than did adults.

Thus, reaction times and imaging data together suggest that in children, an immature stage of the brain where excess synapses, possibly as a result of a burst of proliferation, accounts for the poorer performance and extensive and less efficient frontal activation. A pruned and more myelinated adult brain could explain the faster reaction times and focal activation of the PFC, the area crucial to generativity (Frith et al., 1991) and the inhibitory response (Konishi et al, 1999). The Go/NoGo task requires multiple executive functions including working memory and inhibition albeit at a relatively low level. One possibility is that extensive activation in children is a compensatory strategy used while the brain is less efficient in integrating executive functions.

Adolescents are renowned for engaging in risky behaviour. A recent neuroimaging study suggests that differences in brain activation in mesolimbic circuitry during incentive-driven behaviour between adolescents and adults might account for this (Bjork et al., 2004). A group of 12 adolescents and 12 young adults were scanned while they carried out a task that involved anticipating the opportunity for both monetary gains and losses and the notification of their outcomes. Compared with adults, adolescents showed reduced recruitment of the right ventral striatum and right amygdala

while anticipating responses for gains. Activation patterns during monetary gain notification did not differ between groups. This suggested lower activation for motivational but not consummatory components of reward-directed behaviour. To explain risky behaviour commonly associated with adolescence, the authors postulated that adolescents are driven to seek more extreme incentives to compensate for low recruitment of motivational brain circuitry.

Anecdotally, adolescents are known to be poor at decision-making, especially when risk is involved. In an fMRI study that investigated the neural mechanisms that might account for differences between adolescents and adults in decision-making, participants were presented with one-line scenarios (e.g. "Swimming with sharks") and were asked to indicate via a button press whether they thought this was a "good idea" or a "not good idea"(Baird et al., 2005). There was a significant group by stimulus interaction, such that adolescents took significantly longer than adults on the "not good idea" scenarios relative to the "good idea" scenarios. Furthermore, adults showed greater activation in the insula and right fusiform face area compared to adolescents, during the "not good" ideas. On the other hand, adolescents showed greater activation in the DLPFC during the "not good" ideas and there was a significant correlation between DLPFC activation and reaction time. It was proposed when confronted with a risky scenario, adults' relatively efficient responses were driven by mental images of possible outcomes and the visceral response to those images, in line with the somatic marker hypothesis (Damasio, 1996). However, adolescents relied more on reasoning capacities and therefore activated the DLPFC, hence, the relatively effortful responses compared to adults.

Neural plasticity of the developing brain may underpin different propensities for learning new skills, such as problem solving, at different stages of the life cycle. For example, sensitive periods for learning phonemes of one's mother tongue occurs in the first ten months of life (Kuhl et al., 1992) and the ability to learn a second language declines with age (Hakuta et al., 2003). Logical reasoning required to solve mathematical problems activates both PC and FC in both adolescents and adults. An fMRI study that required participants to solve algebraic equations before and after a practise period demonstrated differential activation patterns after four days of learning in adolescents and adults (Luna et al., 2004b; Qin et al., 2004). Both adolescents and

adults showed an increase in prefrontal, parietal and motor activation while solving the equations. Both groups also demonstrated a reduction in prefrontal areas after practice. However, adolescents, as distinct from adults, additionally demonstrated a reduction in parietal regions after the practice period. The authors proposed that the PC represents an 'imaginal' component necessary for this sort of abstract reasoning task. They proposed that after the learning period, the adolescents are less reliant on this area than the adults. However, the directions of cause and effect remain ambiguous. It is unclear whether the adolescents' decrease in parietal activation with practice was a result of an immature PC and hence a higher relative dependence on the PFC. Alternatively, more localised parietal activation in adolescents might indicate an advantage among adolescents for this sort of task; that is, adolescents depend less heavily on more specialised parietal circuitry, compared to adults. Further functional imaging studies combined with behavioural analysis will clarify the significance of focal versus diffuse brain activation patterns for the propensity to learn.

Although several developmental studies emphasise the decrease in frontal activity with age, in others, activity in this and other regions has been found to increase with age. Using a visuo-spatial working memory task, Kwon et al., (2002) found that performance gradually improved with age between seven and 22 years. Age-related changes were found in several brain regions including the DLPFC and the posterior PC bilaterally. Activity in these regions increased with age on this task. Age predicted activity in these brain regions more than task performance. Similarly, Rubia et al., (2001) reported increased activation in various frontal and parietal regions on a task of response inhibition. Using the Stroop colour-word interference paradigm, which involves inhibition of inappropriate responses, Adleman et al., (2002) observed age-related increases in activity in a left frontal-parietal network of areas. They found no evidence of decreased activity with age.

A recent longitudinal MRI study of participants aged between three and 29 years revealed that the trajectory of change in cortical thickness is associated with the development of IQ (Shaw et al., 2006). The relationship between cortical thickness and IQ, as indexed by Wechsler intelligence scales, was found to vary with age. In early childhood, IQ and cortical thickness throughout the PFC and in the left superior/middle temporal gyri were positively correlated for both males and females, whereas in late

childhood and beyond, the same correlation in these areas was negative. Stratification of participants into three IQ bands (superior (IQ range: 121-149), high (IQ range: 109-120) and average (83-108)) indicated that the maximum trajectory differences between groups were in superior frontal gyrus bilaterally extending into the MPFC. The developmental shift in trajectory was most pronounced for the most intelligent children and adolescents: the highest IQ children had a thinner cortex in early childhood but cortical thickness then increased, peaking at around age 11, and then undergoing the most dramatic cortical thinning thereafter. Shaw and colleagues therefore propose that intelligence levels relate to how the cortex changes during development. They also suggest further investigations including animal studies, to identify the cellular processes that underlie the changes in cortical thickness. This study suggests a direct link between IQ and dynamic properties of cortical structure and also addresses individual differences. Whether increased plasticity relates to better performance on executive function and other cognitive tasks remains to be explored.

1.3.1.3. Confounding effects of task performance

One remaining issue is the confounding effect of task performance differences in fMRI studies. If one group's task performance is worse than that of the other group, then any difference in brain activity between the two groups is difficult to interpret. It might cause the difference in task performance, or it might be an effect of these differences. Future studies should attempt to match task performance between groups to avoid this interpretation problem. Another problem with understanding developmental fMRI data is the functional interpretation of increased or decreased BOLD signals in particular regions, given that we know the brain is developing structurally. If there is an increase in synaptic density at one time point in PFC, for example, and increased blood flow in this area for a particular task, it is difficult to know whether the increased BOLD signal results from higher oxygen demands from greater neural matter at this age compared to at another age, or from a difference in functional strategy at that age.

1.4. Summary

Cross-sectional post-mortem studies in the 1970s/80s demonstrated changes in synaptic density and myelination in FC during childhood and adolescence. Recent cross-

sectional and longitudinal MRI studies show GM and WM changes during adolescence and into early adulthood, with the most prolonged and pronounced changes in PFC, PC and STS. GM decline and WM increase have been interpreted to reflect synaptic pruning and myelination, respectively. Behavioural and fMRI studies show development of executive function skills during adolescence. Executive function is though to rely on PFC. Morphological developments in PFC are thought to correlate with development of cognitive skills relying on PFC and PC, for example, impulse inhibition, willed action and abstract reasoning.

The next section will explore how brain development is linked to social cognitive development in childhood and adolescence and will describe current theories in social cognitive neuroscience that explain how we understand other minds.

DEVELOPING AN UNDERSTANDING OF OTHER MINDS

1.5. Intersubjectivity: current theories from social cognitive neuroscience

1.5.1. What is social cognition?

Intersubjectivity refers to the communication between people that relies on shared meanings (Gallese, 2006). During the last decade, social cognitive neuroscience approaches have been developed to understand how we process sensations, actions and emotions such that we share the meanings of these experiences with others (Ochsner & Lieberman, 2001). Specifically, this branch of neuroscience focuses on the how this shared cognition is instantiated in the brain. Social cognition encapsulates a number of social skills that facilitate complex social interaction in humans. These include the perception of agency, knowledge of the self and the understanding of other people, the last of which is the focus here. Humans are endowed with the capacity to naturally infer intentions, desires, emotions and beliefs of other people, using minimal information. Not only are we typically able to decouple our beliefs from reality, but we can also distinguish other people's thoughts from our own and perceive their mental states from the mere observation of a gesture or a gaze. This intuitive social insight that enables successful interpersonal communication has been labelled "Theory of Mind" (TOM) (Premack & Woodruff, 1978), and the capacity we use to understand other minds is known as "mentalising" (Fletcher et al., 1995; Frith & Frith, 2003). This ability to work out what people might know, think or believe, based on what they say or do, is also referred to as "mindreading" (Baron-Cohen, 1995). Understanding another's mental state enables the understanding of another's intentions, or the ability to take the "intentional stance" (Dennett, 1987) since people's desires and emotions drive their actions. A mentalising mechanism should therefore allow us to intuit someone else's unobservable mental states and thus make predictions of their actions (Frith & Frith, 2006).

1.5.2. The development of social cognition during young childhood

Since the seminal paper by Premack and Woodruff ('Does the chimpanzee have a "theory of mind?"', 1978), much theoretical and empirical work has emerged from the fields of psychology and philosophy to investigate the human ability to mentalise, including the development of experimental paradigms to test this capacity (Baron-Cohen et al., 1985; Dennett, 1978; Wimmer & Perner, 1983). Autism, a developmental

social communication disorder characterised by "mindblindness", or the inability to mentalise, has provided key insights about the processes we typically use to understand other minds (Baron-Cohen, 1995, Frith, 1996; see Chapter 6 for a more detailed account).

The false belief test has also been a crucial paradigm for investigating the development of mentalising (Dennett, 1978; Wimmer & Perner, 1983). Wimmer and Perner designed the first false belief test in which a character called Maxi places a piece of chocolate in a kitchen cupboard and then leaves the room. While he is out, his mother enters the room and moves his chocolate into a drawer, without Maxi seeing. Maxi then returns to the room and the key question is where Maxi will look for the chocolate, in the cupboard or in the drawer (Wimmer & Perner, 1983). The task therefore taps the ability to decouple one's own knowledge from another's knowledge, as well as the other person's belief from a reality. Several variants of this task have since been designed, and such experiments suggest that at age four, children show signs of understanding the scenario, performing at levels higher than chance and by age six, they are able to understand it without any problems. By age six, children are also competent in attributing beliefs about another person's belief, so called second-order false belief tasks (Perner & Wimmer, 1985). TOM appears to be an aspect of social intelligence that is independent of general intelligence (Cosmides, 1989).

Passing a false belief test about another person's belief seems to be closely correlated with passing false belief tests about the self, suggesting shared representations for the self and others (Gopnik & Astington, 1988). It has been shown that children who are able to report their own mental states can also report the mental states of others. Specifically, children were presented with a box for sweets and then shown that there were actually pencils inside it. They were asked 'what Nicky [will] think is in the box?' and then, 'When you first saw the box, before we opened it, what did you think was inside it?'. The ability to answer correctly questions relating to the self was significantly correlated with the ability to answer questions for another person (Gopnik & Astington, 1988). TOM tasks might therefore be measures not only of the consciousness of others' mental states but also of self-consciousness.

While several studies have reiterated findings about TOM, reflecting similar ages for these milestones in the development of social cognition during infancy, less research has been directed to the next major phase of neural plasticity and social development – *adolescence*. As discussed in the previous section, the adolescent cortex, including PFC, PC and STS are subject to structural change during this period. If studies have shown that TOM develops in infancy at around the age of four, what are the cognitive consequences of the continued development of its underlying neural circuitry? Before describing the findings from the few existing studies on social cognitive development at adolescence, the following section will outline recent suggestions about the association of these brain areas with social cognition and their differential roles in mentalising.

1.5.3. How the brain understands other minds

Social neuroscience exploits the advantages of non-invasive brain imaging techniques and integrates approaches from neuroscience, experimental and social psychology to tackle questions pertaining to this kind of implicit social information processing. The majority of studies investigating the role of the brain in social cognition have focused on functioning in the adult brain.

The ability to surmise mental states from simply watching an agent's action or gesture seems to rely on a network of areas in the brain. Several different types of paradigms have been used to test the neural basis of mentalising, involving cartoon strips, stories, moving shapes, and interactive games. Consistently, a network including the temporal poles, the posterior STS/temporo-parietal junction (TPJ) and medial PFC (MPFC) have been associated with tasks in which mainly adult participants are required to mentalise (Frith & Frith, 2003).

An important implicit mentalising task involves showing participants animations of moving shapes. This task established that ordinary adults feel compelled to attribute intentions and other psychological motives to animated abstract shapes, simply on the basis of their movement patterns (Heider & Simmel, 1944). Castelli and colleagues (2000) showed such animations in a study that examined brain activation patterns using positron emission tomography (PET) to contrast sequences where the movements of two triangles were designed to evoke mental state attributions (e.g. one triangle surprising the other or mocking the other), and sequences where the triangles moved

randomly and did not evoke such attributions. This comparison showed activation in the same system, including MPFC, STS and temporal poles, as in other studies with different mentalising tasks.

Interactive games that involve implicit spontaneous mentalising have also been used in brain imaging experiments. For example, in one study, volunteers were scanned while they played a prisoner's dilemma type game with another person (McCabe et al., 2001). In this game mutual cooperation between players increased the amount of money that could be won. In the comparison task the volunteers were led to believe that they were playing with a computer that used fixed rules. A comparison of brain activation during the game task and the comparison task revealed activity within the MPFC.

MPFC was also activated when participants played 'Stone–Paper–Scissors,' a competitive game in which success depends upon predicting what the other player will do next (Gallagher et al., 2002). Again, the comparison condition was created by telling the volunteers that they were playing against a computer. In fact, the sequence of the opponent's moves was the same in both conditions. Participants described guessing and second guessing their opponent's responses and felt that they could understand and 'go along with' what their opponent, but not the computer, was doing. The MPFC was activated only when the volunteers believed that they were interacting with another person.

There have been several fMRI studies that have investigated TOM processes. These have consistently highlighted the involvement of three brain regions in understanding other people's mental states. The medial FC in the region of the paracingulate cortex, the temporal poles adjacent to the amygdala, and the STS near the TPJ, are consistently activated by mentalising tasks that have involved a wide variety of tasks and stimuli.

In one of the first functional neuroimaging studies that investigated TOM processes, participants were asked whether another person from a different era (Christopher Columbus) would know how to use modern objects (such as a hairdryer or food blender) or ancient objects (such as a pre-fifteenth century hunting tool). In order to surmise whether Christopher Columbus would have understood how to use a certain tool, the participants would presumably have to think about Columbus's knowledge.

MPFC and left STS were activated by this mentalising task compared with a control task in which participants made inferences about how to use novel objects (Goel et al., 1995).

Similar activation patterns were found in functional neuroimaging studies in which participants made decisions about mental states of people in stories or cartoons (Brunet et al., 2000; Fletcher et al., 1995, Gallagher et al., 2000). In a PET study, participants were scanned while they performed story comprehension tasks that required the attribution of mental states (Fletcher et al., 1995). In one such story participants had to work out that the protagonist's action (a robber giving himself up to the police) was based on his false assumption about the policeman's beliefs (that the policeman knew he had robbed a shop). This task required mental state attribution because the beliefs of the robber and policeman were not made explicit in the story. When compared with comprehension tasks involving 'physical' stories that did not require mental state attribution, the TOM task produced activation in the left medial frontal gyrus (Fletcher et al., 1995).

Using the same stories and fMRI, Gallagher and colleagues (2000) found that the medial frontal gyrus, the STS and temporal poles bilaterally were activated by the TOM stories. In addition, these regions were also activated by non-verbal cartoons that involved mental state attribution in order to be understood (Gallagher et al., 2000). Similarly, the STS and medial frontal gyrus were activated in a PET study in which participants were instructed to choose the right ending for a series of cartoons only when this required mental state attribution and not when it required physical reasoning (Brunet et al., 2000).

These brain areas are also engaged when participants make semantic decisions about other people's characteristics. In an fMRI study, participants were presented with stimuli from three different categories (people (e.g. Mary); fruits (e.g. banana); clothes (e.g. mittens), adjacent to adjectives (e.g. curious; pitted; woollen), and asked whether the adjective could be used to describe the item in the stimulus (Mitchell et al., 2002). While semantic judgements about objects activated inferotemporal cortex and ventrolateral PFC, judgements about other people were associated with activity in MPFC, right TPJ, STS and fusiform gyrus, suggesting distinct sets of brain areas that

are linked to knowledge about other people compared to that required for inanimate objects (Mitchell et al., 2002).

A subsequent fMRI study investigated the specificity of these neural representations for knowledge about other people, by comparing brain activity during semantic judgements about other people and about dogs (Mitchell et al., 2005). For each of these two types of target, participants were again required to make judgements about the applicability of words to psychological states or to physical parts of the body of the target (person or dog). The words that could be used to describe people (e.g. curious) were designed to be equally applicable to dogs. Two important findings emerged from the imaging data: firstly, that higher MPFC activation was associated with judgements of psychological states relative to body parts, and secondly that this MPFC activity effect extended to dogs as well as people. This suggests that MPFC has a specific role for understanding mental states, rather than being generalisable to all kinds of person perception but that this role of MPFC can be generalised to another person or a dog, that is, another mental agent (Mitchell et al., 2005). Action knowledge (represented by verbs which applied to both people and dogs, e.g. run or bite) about people, however, activates distinct brain areas to action knowledge about dogs (Mason et al., 2004). Participants were scanned using fMRI while making semantic judgements about the relevance of the verbs to dogs or people, and results indicated that while action knowledge about dogs elicited activity in occipital and parahippocampal gyri, equivalent judgments about people was associated with increased activity in MPFC (Mason et al., 2004). MPFC, therefore, has consistently been linked to social cognitive processing.

There is emerging neuroimaging evidence for differential roles of each of these areas. Firstly, the STS/TPJ has been implicated in the ability to see the world from another person's point of view (Aichhorn et al., 2006) (i.e. *What does she think from her perspective?*). Most likely, this is because of its role in eye-movement observation (Pelphrey et al., 2004) and in the representation of the body in space (Blanke et al., 2005). The TPJ is associated with false belief tasks (Apperly et al., 2004) and the temporal poles are involved in the storage and use of knowledge of the world (Funnell, 2001) (i.e. *What would she* tend *to think, given the circumstances*?). Finally, a large number of studies have linked social cognitive processing with medial PFC (MPFC) (including the anterior cingulate cortex (ACC). Based on experimental data and an

analysis of the anatomical connectivity of the MFC, Amodio and Frith (2006) have recently suggested that self-reflection, mentalising and person perception are all associated with MFC. Different subdivisions are dedicated to different processes such that caudal regions are associated with monitoring actions, orbital regions with outcomes, while the more anterior regions are related to meta-cognitive processes, or "thinking about thinking" (i.e. *"What would she think, given how she feels, in the context of how I feel?"*) (Amodio & Frith, 2006).

1.5.3.1. Theories of theory of mind

Thus, for normal social behaviour, it is necessary that social cognitive processes coordinate the implicit understanding of other people's mental states. In other words, TOM needs to occur automatically in order for each 'player' in a social interaction to successfully explain, predict and manipulate other people's behaviour in everyday life (Humphrey, 1976). Several psychologists have highlighted the evolutionary importance of social cognition. For example, Baron-Cohen underlines the importance of a fast and effective mindreading system for 'making inferences about whether [another's] motives are purely altruistic' and for detecting social threats (Baron-Cohen, 1995). In fact, Barresi and Moore (1996, pp. 107) suggest that,

> 'the evolution of intelligence in primates that ultimately led to human beings was driven in part by the demands of social information processing'.

In the last 15 years, several theories of TOM, and their variants, have been put forward to account for the mechanisms that underlie the ability to read other minds. These have tended to fall into two categories: theory theory and simulation theory. Theory theorists believe that our understanding of other minds rests on our knowledge of a theory, analogous to a scientific theory. In other words, theory theory states that we process a folk psychological theory comprising laws and rules that can be applied to everyday life in order to explain behaviour (e.g. Carruthers, 1996; Gopnik & Meltzoff, 1997). In contrast, simulation theory denies the deployment of a set of laws and rules to understand others. Put simply, simulation theorists claim that we use our own mental processes to simulate others and thus understand their actions and mental states (e.g. Gallese & Goldman 1998; Heal, 1995). Simulation theory has gained increasing credence recently, since the discovery that a set of neurons in the primate brain simulate

electrical activity of other conspecifics (see Rizzolatti & Craighero, 2004). This will be described in more detail later in this chapter.

1.5.4. The consequences of atypical mentalising

The finding that autistic children have specific difficulties with TOM tasks (Baron-Cohen et al., 1985) has been instructive for the understanding of the function and development of TOM in typical and atypical populations. Impairment in TOM, or an inability to mentalise, has been proposed to account for the social communication problems seen as one of the hallmark features of autism (Frith et al., 1991; see Chapter 6 for a detailed discussion of autism and social cognition). In fact, Bleuler originally used the term "autism" to refer to an aspect of schizophrenia. This aspect was also described as "autistic aloneness" or the withdrawal from other people into the self (Bleuler, 1911). It is thought that this also manifests itself as an inability to correctly infer other people's perspectives or intentions (Frith, 2003). Autistic people have difficulty in recognising that other people may have a different understanding of the world to themselves. Thus, they appear to lack a TOM. The behavioural phenotypes of autism and schizophrenia are very different. Firstly, autism can be diagnosed in early childhood whereas schizophrenic symptoms tend to first manifest themselves in late adolescence or early adulthood. Furthermore, while a "deficit" in TOM might lead to the social behavioural symptoms of autism, the qualitative impairment in schizophrenia is quite different. Schizophrenic patients with positive symptoms such as delusions of persecution have no difficulty in understanding that other people have intentionality and emotions, as distinct from their own. However, they tend to over-interpret other people's intentions, and to read them as directed towards themselves (Frith, 1992). These two very different qualitative impairments in TOM in autism and schizophrenia might be conceptualised as different forms of egocentrism or appreciation of "other-ness" that are on two different ends of a continuum (Frith, 2004). The social communication feature of autism, "mindblindness", might be characterised by poverty in the appreciation of another person's mind, or a bias towards the self. Delusions in schizophrenia might thus be characterised by an over-appreciation of "other-ness" at the extreme other end of this spectrum, leading to a tendency to over-attribute agency and intentionality to others, that might not even be animate (Frith, 2004). Mentalising in schizophrenia and autism will be discussed further in later chapters (see Chapters 3 and 6).

1.6. Development of emotion processing during adolescence

The environmental and biological changes at adolescence lead to new social encounters and heightened awareness and interest in other people. The importance of evaluating other people may be associated with increased attention to socially salient stimuli, particularly faces, and the processing of emotional information. Recognition of facial expressions of emotion is one area of social cognition that has been investigated during adolescence (see Herba & Phillips, 2004). fMRI studies support the notion that development of brain regions are linked to the development of emotion processing. The amygdala, which has consistently been associated with emotion processing (Adolphs, 1999; Dolan, 2002; Phillips et al., 2003), was found to be significantly activated in response to the perception of fearful facial expressions in an fMRI study of 12 adolescents aged between 12 and 17 (Baird et al., 1999). Similarly, the perception of happy faces compared with neutral was associated with significant bilateral amygdalar activation in a group of 12 adolescents aged 13 to 17 (Yang et al., 2003). Sex-differences in amygdala-mediated cognitive development have also been reported to occur during adolescence (Killgore et al., 2001). In this fMRI study, while the left amygdala responded to fearful facial expressions in all children, left amygdala activity decreased over the adolescent period in females but not in males. Females also demonstrated greater activation of the DLPFC over this period, whereas males demonstrated the opposite pattern. These findings were taken as evidence for an association between cerebral maturation and increased regulation of emotional behaviour; the latter mediated by prefrontal cortical systems. It is possible that functional maturation associated with face emotion processing may be modulated by gender-specific hormonal profiles.

The effect of age was addressed by Thomas and colleagues (2001) in their investigation of amygdalar response to fearful facial expressions in two groups: a group of children (mean age 11 years) and adults (mean age 24). Adults relative to children demonstrated greater amygdala activation to fearful facial expressions, whereas children relative to adults showed greater amygdala activation to neutral faces. It was argued that the children perceived the neutral faces as more ambiguous than the fearful facial expressions, with resulting increases in amygdala activation to the neutral faces. Age-related differences in neural strategies for emotion processing have been shown in an

fMRI study of a group of adolescents (aged seven to 17) and a group of adults (aged 25-36) who viewed faces showing emotional expressions. While viewing faces with fearful emotional expressions, adolescents exhibited greater activation than adults of the amygdala, OFC and ACC (Monk et al., 2003). When participants were asked to switch their attention between a salient emotional property of the face, like thinking about how afraid it makes them feel, and a non-emotional property, such as how wide the nose is, adults, but not adolescents, selectively engaged and disengaged OFC. In other words, adults better modulate OFC activity based on attention demands, while adolescents better modulate activity based on emotional demands. On the other hand, when there were no attentional demands, emotional content of the stimuli induced higher activity in ACC, OFC and amygdala among adolescents compared to adults. These fMRI results suggest that both the brain's emotion processing and cognitive appraisal systems develop during adolescence. This development has previously been interpreted in the context of the Social Information Processing Network model (cf. Nelson et al., 2005).

1.6.1. The Social Information Processing Network (SIPN) model

This model posits that social information processing occurs by way of three interacting neural "nodes", which afford the detection of social stimuli that are then integrated to a larger emotional and cognitive framework. Nelson and colleagues (2005) propose that the 'detection node' comprising the intraparietal sulcus, the STS, the fusiform face area as well as temporal and occipital regions, deciphers social properties of the stimulus such as biological motion. The 'affective node', including limbic areas of the brain including the amygdala, ventral striatum, hypothalamus and OFC, is then thought to process the emotional significance of the social stimulus. Finally, the 'cognitive-regulatory node', consisting of much of the PFC, is responsible for TOM, impulse inhibition and goal-directed behaviour (Nelson et al., 2005). The development of the nodes, that is the connections between them, the innervation by gonadal steroid receptors and the maturation of the neural substrates themselves, during adolescence are proposed to explain development of social cognitive behaviours.

A similar triadic model has been proposed to govern motivated behaviour. This model includes the ventral striatum, for supporting reward processes and approach behaviour, the amygdala for its role as a "behavioural brake" that mediates avoidant behaviour and the PFC as a supervisory area that orchestrates the other processes (Ernst et al., 2005).

Ernst and colleagues suggest that the balance between reward-driven and harm-avoidant behaviour is tilted towards the reward-driven end in adolescents. This is hypothesised to be due to either differential strength in the reward and avoidance systems in adults and adolescents (in terms of neural systems) and/or poorer regulatory control in adolescents.

Thus, only a handful of studies have recently investigated social information processing during adolescence. However, these studies, reviewed above, have employed tasks that tap the perception of emotional stimuli. So far, however, none has investigated social cognitive *communicative* processes per se, that involve engaging with other people's minds and tuning into their thoughts. Furthermore, few have considered the development of the mechanisms by which we understand others. The next section describes a recent idea that actions have a special role in social understanding.

1.7. The role of the motor system in social interaction

1.7.1. Shared representations for perception and action

During the last decade, evidence has accumulated from experiments in non-human primates, as well as in humans, in support of the idea that the perception and execution of one's own actions, as well as the understanding[1] of another agent's actions, are functionally connected, relying on a common coding system and shared neural systems in the brain. In fact, in his ideomotor theory of action, William James in the 19th century claimed that "every mental representation of a movement awakens to some degree the actual movement which is its object" (James, 1890). The implication is that perceiving an action, that is, observing, imagining or in any way representing an action activates the motor programs used to execute that same action (Jeannerod, 1994; Prinz, 1997). As such, it has long been thought that cognition is embodied in action (see Merleau-Ponty, 1962).

1.7.2. Mirror neurons: a mechanism for matching observation and execution of actions

The discovery of "mirror neurons" (MNs) in the ventral premotor cortex (VPMC) of the macaque monkey lends neurophysiological support to the common coding theory between perception and action, and furthermore, suggesting that these shared

[1] By "understanding", I refer to the knowledge of another person's actions, which includes the conscious or unconscious interpretation of or engagement in another's movements.

representations are fundamental to the social interaction between self and other. MNs in area F5 of monkey premotor cortex, were found to discharge both when the monkey *performed* a goal-oriented action and when it *observed* another agent performing the same object-directed action (Di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996a). MNs respond selectively to goal-directed biological motion, discharging only during the observation of hand-object interactions and not in response to the same 'action' performed by a mechanical tool, such as a pair of pliers (Rizzolatti et al., 2001). In the F5 region of the monkey brain, MNs appear to represent mainly hand and mouth actions, and show congruence between the visual actions they respond to and the motor responses they code (Gallese et al., 1996). Neurons that respond to the observation of others' action have also been located in the monkey STS (Jellema et al., 2000; Perrett et al., 1989; 1990). These neurons respond to the observation but not the execution of other agents walking, moving their arms or turning their head as well as goal-directed hand movements (Perrett et al., 1990). Neurons, which are excited both by observation and execution of actions, are also found in the rostral part of the inferior parietal lobule (IPL) (Fogassi et al., 1998; Gallese et al., 2002) in the macaque. MNs in the IPL not only fire during the observation of an act (e.g. grasping), but also before the beginning of the following act that specifies the action (e.g. eating). It was therefore suggested that MNs in the IPL code the observed motor act as well as the observed agent's intentions (Fogassi et al., 2005).

1.7.3. The transformation of visual information into knowledge: mirror neurons and action understanding

A further set of experiments suggested that MNs mediate action understanding, such that the monkey can interpret the *meaning* of an action in the absence of the visual cues that trigger MNs. Umiltà and colleagues (2001) demonstrated that neurons respond not only during the observation of a full object-directed grasping action but even when the final part of the grasping action was hidden from the monkey's vision. Half of these MNs responded with equal intensity to both the observation of the full action and the hidden action. This finding indicated that it is the meaning, rather than the visual features, of the action that the neurons respond to. In addition, it was found that 15% of neurons in the monkey F5 region respond both to the sight of a noisy action such as a paper being ripped as well as the sound of the action alone (Kohler et al., 2002). Similarly, these results suggest that when the monkey is presented with sufficient clues

to create a mental representation of the action, MNs are activated. In other words, MNs "know" what the actions of others mean.

1.7.4. The human mirror neuron system

There is now strong neurophysiological evidence for the existence of analogous motor resonance phenomena in humans. For example, studies using electroencephalography (EEG), which measures electrical activity in the brain and magnetoencephalography (MEG), which makes sensitive measurements of the magnetic fields produced by neuronal activity, demonstrate that desynchronisation of the mu rhythm occurs both during the subject's own movements as well as the observation of other people's actions (Altschuler et al., 1997; 2000; Cochin et al., 1998; 1999; Hari et al., 1998). Similarly, transcranial magnetic stimulation (TMS) has shown that simply observing a movement has measurable effects on the peripheral motor system (Fadiga et al., 1995). The left primary motor cortex of participants was stimulated using TMS while participants watched the experimenter either grasping objects (transitive movements) or performing meaningless arm movements (intransitive movements). This led to an increase in the amplitude of the motor evoked potentials (MEPs) in specific hand muscles, relative to the control conditions when participants watched an object moving. The facilitation of MEPs during action observation occurred in those muscles that would be used for the execution of the observed movements. For example, listening to speech sounds which strongly involve tongue movements when spoken, elicits an increase in MEPs in the listener's tongue muscles (Fadiga et al., 2002).

Numerous fMRI studies have shown that several brain areas are activated by the observation of actions performed by others, including, crucially, the rostral part of the inferior parietal lobule, the lower precentral gyrus and the posterior part of the inferior frontal gyrus (e.g. Buccino et al., 2001; Decety et al., 1997; Grafton et al., 1996; Grèzes et al., 2001; 2003; Rizzolatti et al., 1996b; Stephan et al., 1995). Buccino and colleagues (2001) demonstrated that the frontal and parietal mirror regions are somatotopically organised, such that watching mouth, hand, and foot movements alone (without objects) activates the same functionally specific regions of premotor cortex as making those respective movements. Furthermore, when actions were directed to objects, the PC became activated. Again, functionally specific regions of the PC were activated according to the object-directed action being performed. Interestingly, unlike in

monkeys, the human mirror neuron system (MNS) is activated by the observation of both transitive and intransitive movements, although the former type is associated with both parietal and frontal activation while the latter by just frontal activation (Iacoboni et al., 1999; 2001). In addition, EEG has been used to show that motor activity in the brain is also elicited prior to observing someone else's action (Kilner et al., 2004). The readiness potential, an electrophysiological marker of motor preparation, is not only present during action observation but also *prior to* the onset of the observed action. The authors suggested that this signifies action prediction and the notion that the knowledge of an upcoming action is enough to excite the motor system of the observer. It was speculated that this might occur because it is an advantage for the brain to anticipate, rather than simply react to, another person's action (Kilner et al., 2004).

1.7.5. Observation-execution mapping in the human brain

Human motor resonance in the brain is modulated by the type of observed action, and whether it belongs to the observer's own motor repertoire (Buccino et al., 2004). When human participants were scanned using fMRI during the observation of video clips of biting and oral communicative actions performed by a man, a monkey or a dog, actions that did not belong to the motor repertoire of the observing subject did not trigger the motor system. For example, the observation of biting performed by a man, a monkey or a dog elicited activity in the inferior parietal lobule and the pars opercularis of the IFG as well as the precentral gyrus. The observation of communicative gestures elicited progressively lower frontal activation as the observed action became increasingly non-human. Speech reading therefore activated IFG, while observation of the monkey specific communicative gesture of lip-smacking produced less frontal activity and barking did not elicit any frontal activity. These results suggest that humans map observed actions onto their own motor system, so long as the observed actions belong to their personal motor repertoire. When the observed action is foreign to the observer's motor repertoire, the observation of the action does not engage the motor system. The action is therefore seen, but not "known". Semantic knowledge about actions appears to be represented in a category-specific way such that regions in the motor cortex are recruited both during execution of movements of body parts (e.g. foot), and when action words that correspond to the body part (e.g. kick) are simply read (Hauk et al., 2004).

It is proposed that the MNS activity during action observation corresponds to an action representation[2] in the observer's brain, of the actor's action (Gallese et al., 2004; Rizzolatti et al., 2001). The action representation matches that which is generated during the action execution of the observer. The motor outcome of that action representation is known to the actor. As such, the representation held by the MNS during action observation can predict the outcome of another's actions. Knowledge of another's actions is thus translated to knowledge of another's intentions.

1.7.6. The mirror neuron system as a bridge between minds

The brain, therefore, tunes into others during the observation of their actions. It is argued that this level of motor attunement forms the basis of a much more profound form of interpersonal engagement: social cognition. The human brain is subconsciously "interested" in other people at the level of action. How might this relate to our social interest in other people? First of all, behavioural studies have shown that the human motor system is geared up for making the actions it observes. The common coding between perception and action gives rise to a motor priming process whereby human participants preferentially respond to the observation of a human arm compared with a robotic arm, in terms of lower reaction times or higher brain activity (Castiello et al., 2001; Perani et al., 2001). In line with this notion that like-actions in like-others activate one's own motor system, psychophysical studies also show an interference effect such that if a subject who is performing an arm movement watches a robot or a human perform congruent and incongruent actions, the observation of the human, but not the robot, making incongruent actions interfere with the observer's action execution (Kilner et al., 2003). Such findings indicate that the observation of kinematically and visually similar actions in others elicits a similar response in the observer. It has been proposed that this motor facilitation might underpin social facilitation, that is, the notion that the presence of others appears to impact on our own actions (Jackson & Decety, 2004; Sebanz et al., 2003).

[2] An action representation refers to a schema or internal model, which is composed of information from one's own cognitive mechanisms as well as from the external world, a simulation or copy of an actual action (Jeannerod, 1997; Neisser, 1976); see Chapter 5 on Action Representation for a fuller description.

1.7.7. The mirror neuron system as a mechanism for simulation and imitation

Evidence has accumulated, therefore, that we directly map visual representations of actions we see onto our own motor representation for those actions, and the higher the degree of similarity between the features of the observed action and those of our own motor repertoire, the more strongly we are primed for the action. As a consequence, we sometimes imitate others' actions, without even being aware of it (Tessari et al., 2002). This suggests that the MNS might facilitate our natural tendency to imitate. Indeed, not long after birth, babies will spontaneously imitate actions of adults they observe (Meltzoff & Moore, 1977). It is proposed that by 14 months, infants' imitation is not simply emulation. In a replication of an earlier study (Meltzoff, 1988), infants of the same age showed an ability to evaluate the rationality of the strategy of an action (the means to a goal) (Gergely et al., 2002). The paradigm required infants to watch a demonstrator using her forehead to illuminate a light-box, and tested the imitation of the means to the goal. Gergely and colleagues modulated the constraints of the action. In one condition, the demonstrator's hands were occupied and in the other they were free. After observing the demonstrator performing the head action when her hands were free, 69% of the infants re-enacted the head action. However, after seeing the adult perform the same task with her hands occupied, only 21% of the infants replicated the head action. It was concluded that infants could rationalise the action. In other words, it appeared to make sense to the infants to perform the action using the head when the hands were occupied, but given that their own hands were free, it was more sensible to achieve the same goal using their hands (Gergely et al., 2002). Infants as young as 14 months are therefore thought to be able to imitate "rationally", that is, they represent the goals of the actions they see and can imitate both the means and the goal of actions (Gergely et al., 2002).

A handful of neuroimaging studies have shown that imitation is associated with much of the same neural circuitry as that which is active for action observation (Grèzes et al., 2003; Iacoboni et al., 1999; Koski et al., 2002; Nishitani & Hari, 2002). For example, in an fMRI study, Iacoboni and colleagues compared brain activity in the observation only and imitation condition while participants watched video stimuli of a moving finger in the scanner. In both these conditions, there was activity in the left *pars opercularis* of the IFG, the right anterior parietal area, the right STS and the right parietal operculum and activity was greater in the imitation, compared with observation condition (Iacoboni

et al., 1999; 2001). Similar brain areas are also activated by the imitation and observation of emotional facial expressions (Carr et al., 2003).

If similar brain networks are triggered when we ourselves act, when we see others act, and when we copy other people's actions, there must be a motor equivalence between what we do and what others do. As such, there is a shared representational space for actions of our own and those of others. Thus, the mirror phenomenon in the brain provides a possible neurophysiological explanation for the long-standing theory of action simulation.

1.7.8. Embodiment, simulation theory and self-other interactions

Conceived most broadly, simulation theory posits that we generate similar mental processes in our own minds in order to understand the actions, beliefs, desires and emotions of another (Gallese & Goldman, 1998). The basis for attributing propositional attitudes such as intentions or beliefs is thought to be the understanding of another person's actions. Thus, simulating another person's action would trigger an action representation from which the underlying goals and intentions could be inferred on the basis of what our own goals and intentions would be for the same action.

The notion that humans have a direct experiential grasp of another person's mind via their actions can be traced in the early twentieth century European movement of Phenomenology. Phenomenological accounts of knowledge privilege experiential accounts, and describe consciousness as embodied and experience as lived (*Erlebnis*, Husserl, 1970). In other words, there is immediacy between the body and the world, such that our understanding of the world is grounded in our corporeal nature (Husserl, 1970). The philosophy of French phenomenologist, Maurice Merleau-Ponty (1908-1961) describes well this proposed intimate relation between the self and world (or, self and other), in which perception is the key to this immediate link. This view would argue that a visual scene, for example, is not understood through the visual system integrating several components of the scene into a neural input (e.g. Fodor, 1982). Instead, the meaning of that which is seen is:

> "constituted in the hold which [the] body takes on it; it is not first of all a meaning for the understanding, but a structure accessible to introspection by the body."

> *(Merleau-Ponty, Phenomenology of Perception, 1962, pp. 369)*

Merleau-Ponty's anti-Cartesian approach therefore saw human consciousness as immersed in the external world. He extended this dialectical thinking to intersubjectivity: the same notion of interrelatedness of self and other is used to explain such behaviours as a baby that will open its mouth on seeing an adult opening his/her mouth. According to Merleau-Ponty, this action reflects *Mitsein*, the idea that we are in a world of others, where consciousness can not be divorced from the external world but exists in a constant dialectic with others.

This description of embodied consciousness is central to simulation theory[3]. Action, which is mapped onto perception, is therefore implicated in higher order cognitive processing that leads us to understand other minds. Several variations of simulation theory exist within the realm of philosophy of mind. It has been suggested that simulation is explicit, involving the positioning of oneself into the "mental shoes" of another and the use of pretend mental states to attribute thoughts and beliefs to that person (Goldman, 2005). There is also debate about whether simulation is the default, or a necessary, mechanism through which we understand others (see Goldman, 2002). Furthermore, some simulation theorists argue that simulating others is implicit and sub-personal, such that is not available to conscious reflection and rooted at the neuronal level (e.g. Gallese & Goldman, 1998; Grèzes and Decety, 2001; Rizzolatti et al., 1996a; 2000). As proposed in Gallese's "shared manifold hypothesis" we understand others by modelling their action, and this can be distinguished at the phenomenological (experiential), functional and neuronal levels (Gallese, 2001, pp. 45 (italics inserted)):

> "The *phenomenological* level is the one responsible for the sense of similarity...that we experience anytime we confront ourselves with other human beings. It could be defined also as the empathic level...The *functional* level can be characterized in terms of simulation routines, as if processes enabling models of others to be created. The *subpersonal* level is instantiated as the result of the activity of a series of mirror matching neural circuits."

[3] Fundamentally, phenomenologists reject the role of representation in their accounts of knowledge. Given the notion of immediacy between the self and other via perception, there is no place for representation (Merleau-Ponty, 1962). However, I have described evidence and theory from cognitive neuroscience studies which argues that *representation* of action, or the internal modelling of an action, is indeed what provides a shared space between self and other.

It is this latter view of implicit simulation that is endorsed in this thesis. While the accounts and hypotheses here remain agnostic about alternative terminologies (e.g. "enactive perception" (Noë, 2005) or "passive elicitation" (Gallagher, 2006), and about whether simulation is the default mechanism or the only mechanism of interpersonal understanding (see Jacob, 2002, for a discussion of hybrid models), in line with above evidence from MNS theories, a premise of the experiments which follow is that motor resonance or action simulation is *involved in* interpersonal understanding. According to this theory, the activation of the MNS in the observer's brain is believed to correspond to an action simulation – a copy or representation of the actual action that is being observed.

1.7.9. The link between action understanding and social understanding

1.7.9.1. Actions as a means to intention understanding

It appears that the mirror system is involved in understanding the "global" intentions of other people's actions, beyond the immediate goal of a movement (Iacoboni et al., 2005), such as the symbolic meanings of simple hand actions (Nakamura et al., 2004). In an fMRI study of 23 adults, Iacoboni and colleagues (2005) investigated the influence of the *context* of an action on activity in the mirror system. Participants in the scanner were presented with video clips that were organised into three main conditions around the theme of drinking tea: Context (consisting of scenes in which actions occurred, without the action, but with the objects, e.g. a tea cup surrounded by a teapot, biscuits, a plate); Action (consisting of a goal-oriented action without any context, e.g. a hand grasping the tea cup) and Intention (consisting of the goal-oriented action embedded in the context, e.g. a hand grasping a tea cup in the context of the teapot, biscuits, plates, etc.).

Both the Action and Intention conditions, compared to the resting condition, yielded a significant signal increase in the parieto-frontal and STS regions typically associated with the execution, observation and imitation of hand actions. The Context condition elicited activity in similar areas, although not in STS or the inferior parietal lobule, most likely because there was no biological action in this condition. Compared to the Action only and the Context only conditions, the Intention condition, in which participants viewed the hand grasping the teacup in the "tea drinking" context, elicited significantly

higher activity in the *pars opercularis* of the inferior frontal gyrus and in the part of the VPMC in which hand actions are represented. Differential signal increase in inferior FC in the two different contexts suggested that the higher activity in the Intention condition was not simply due to the presence of objects. The authors proposed that "logically related" neurons in this area, which are additional to the classically described MNS, are triggered by the observation of an initial part of the action, which codes the intention (e.g. bringing to the mouth cues understanding of the intention that "he *wants* to drink"), when embedded in a specific context. When we seen an action, therefore, in a particular context, our motor system recognises the chain of motor acts that is typically carried out in that context to accomplish a goal. The mirror system is therefore able to recognise the intentions driving the action. In the same way that Merleau-Ponty describes gestural communication, "it is as if the other person's intention inhabited my body and mine his" (Merleau-Ponty, 1962), the MNS therefore code both the "what" and the "why" of other people's actions.

1.7.9.2. Actions as a basis of empathy

Given the brain's similar involvement in both first- and third-person experiences of actions, intentions and emotions, the mirror-matching mechanism is also thought to underlie the human propensity to empathise with other people's sensations or emotions. The notion of empathy as *Einfühlung*, literally translated from German as, "feeling into" (Titchener, 1909) has been the subject of much discussion in the social sciences, for example, in aesthetics, where *Einfühlung* first described the idea that a work of art could bring about physical and emotional changes in the viewer that correspond to that which is expressed in the art (Vischer, 1873). The German psychologist, Theodore Lipps' use of *Einfühlung* describes how the perception of an emotional gesture in another person directly activates the same emotion in the perceiver. This view, espoused by simulation theorists, would correspond to the finding that perception-action mapping facilitates a direct arousal of emotions in the observer, matched to the person who is observed.

Disgust has been relatively well studied using fMRI. The feeling of disgust in response to the taste or smell of disgusting stimuli has been associated with elevated activity in the insula (Royet et al., 2003; Zald & Pardo, 2000). The anterior insula is also activated by the observation of facial expressions of disgust in other people (Phillips et al., 1997; Wicker et al., 2003). Futhermore, the amplitude of the insular response is modulated by

how intensely disgusted the facial expressions appear (Phillips et al., 1997). This phenomenon is known as emotional contagion. It is lost when there is damage to the associated brain areas. A lesion to the left insula has been shown to selectively impair both the visual and auditory recognition of disgust in other people (Adolphs et al., 2003; Calder et al., 2000). In addition, the patient in these lesion studies reported a blunted sensation in his own first person experience of disgust. One's own brain thus becomes active by the recognition of another's disgust, *as if* we ourselves were experiencing the sensation.

Neuroimaging studies demonstrate common brain activity for the self and the other during the empathic experience of another in pain (Jackson et al., 2005; Singer et al., 2004). Singer et al. investigated pain-related empathy in 16 couples, by measuring brain activity in the woman using fMRI, while painful stimulation was applied to her or to her partner's hand. Both her and her partner's hands were made visible to the female partner. A factorial design with four conditions of Painful, Non-Painful, Self and Other was employed and the comparison between pain-related brain activity in the Self and Other condition indicated that part of the "pain matrix" was automatically triggered in the brain of the female during the knowledge that her partner was being subjected to pain.

Specifically, when participants received pain and during the knowledge of their partner's pain, bilateral anterior insula (AI), rostral ACC, brainstem and cerebellum were activated. In addition, empathy scales indicated that there was a correlation between empathy-related brain activity in the AI and ACC and subjective experiences of pain. Activity in AI and ACC was therefore common to both the Self and Other condition. However, empathy for the partner's pain involved only the affective, but not the sensory component of the brain's pain matrix. It was argued that the involvement of context-dependent affective aspects, but not the sensory-discriminative aspects, of pain reflect the automatic triggering of emotional representations of one's own subjective feelings to engage with the feelings of others. Preston and de Waal (2002) have integrated evidence and theory across various disciplines spanning developmental psychology, social psychology, evolutionary theory and neuroscience, to the Perception-Action Model (PAM), can explain empathy in various species, age groups and in human empathy disorders. In line with the motor theory of social cognition that

has emerged since the discovery of the MNS, the PAM places special importance on action as a mode through which self and other can identify with one another, mediated by neural circuitry and physiological processes that are involved in the execution of one's own actions, the observation of another's action, the experience of emotions and the affective engagement in other people's emotions (Preston & de Waal, 2002).

1.7.10. The problem of action identity: agency and authorship

If my brain 'mirrors' observed actions, how do I know that it is someone else, and not me, who is moving when I observe an action? In other words, 'what gives me the right to speak of an 'I,' and indeed of an 'I' as a cause...' (Nietzsche, 1886)? The human subjective experience of freely willed action requires that the actor feels a sense of agency. In other words, the action is one that the agent can own, 'bearing [one's] signature' (Pettit, 2001). In the following section, I outline how a sense of self might emerge from representations of action. How do we feel in control of our actions? The ability to attribute one's own actions to the self is crucial to feeling that the experience is 'mine'. Important hypotheses have been built from studies that have investigated how we recognise the consequences of our actions and how this 'self-monitoring' system distinguishes between self and other. In addition, studies of patients with disorders of volition provide evidence that a breakdown in the self-monitoring system may account for a disturbance to the normal experiential link between intention and the awareness of volitional control.

1.7.10.1. Distinguishing between self and other through prediction

Being aware of one's own actions and distinguishing them from the actions of others is critical for feeling a sense of self and for communication with other agents. Usually, when we carry out an action, we *feel* a sense of agency - that is, we feel that we are both the author and owner of our own action. How is this feeling of ownership possible? This is particularly problematic given the well established mirror in the brain. Evidence from motor control studies suggests that the brain solves the problem of agency through prediction.

1.7.10.2. Forward models

It has been proposed that internal motor representations, also known as forward models, serve as predictors in the brain (Miall & Wolpert, 1996; Wolpert & Flanagan, 2001).

Prediction is a necessary step in motor planning and can be used in many ways, for example, for fine motor adjustments, action planning and motor learning. Several studies have suggested that, through the anticipation of future outcomes of actions, the brain links the consequences of a movement to the prior intention, to confer a sense of agency.

For every intended action, the brain must issue a motor command to the muscles in order to execute the action. It is proposed that a duplicate of the motor command - or 'efference copy' - is generated in parallel and used to make predictions about the sensory consequences of one's own action. The *forward dynamic model* predicts the sensory consequences of the movement and compares them with the desired effects, for example, the intended position of a hand. Discrepancies between predicted states and desired states result in error signals that can be used to fine-tune actions. A controller, also called an *inverse model*, gauges this relationship to provide the motor instructions required by the muscles to achieve the desired effect, such as a particular grip force for a given object. The *forward output model* predicts the sensory consequences of the motor act and compares them with the actual effect of the movement. Discrepancies between predicted states and actual states can be used for self-monitoring, that is, to distinguish between self-produced or externally produced actions, and in doing so maintain a distinct sense of self (Figure 1.5).

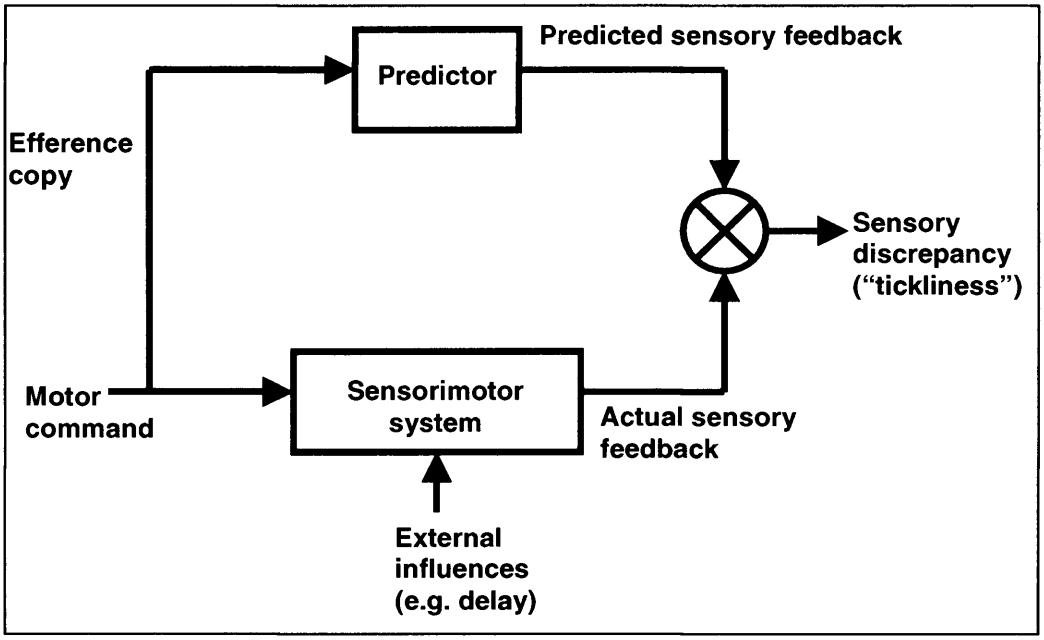

Figure 1.5. ***Forward model.*** *An internal predictor uses information about movements to distinguish between self-produced and externally-produced sensations (adapted from Blakemore et al., 2000).*

1.7.10.3. Recognising the consequences of action

This predictive control model may account for why we experience self-produced touch differently to a touch stimulus produced by an external agent or object. For instance, it is well known that you cannot tickle yourself. Why do we react differently (or not at all) to a self-produced tickle compared to an externally-produced tickle? A series of studies provide evidence that self-produced stimuli are perceptually attenuated whereas externally produced stimuli are not. In one experiment, a device was used to deliver a touch stimulus to the palm of the subject's right palm. In the first condition, participants produced the stimulus themselves, using the left hand, while in the second condition, the experimenter delivered the stimulus. Participants consistently rated the self-produced touch as less tickly and intense than the externally produced touch (Blakemore et al., 1999). This may be explained in terms of the framework of motor control outlined above. The forward output model can be used to make accurate predictions of the sensory outcome (in this case, the tickly sensation of the stimulus) of a self-produced action, using the motor command and efference copy. This results in an attenuation or cancellation of the sensory outcome. In contrast, for an externally generated sensation, there is no efference copy available upon which to base a prediction, and hence, no attenuation. As a result, externally produced sensations are effectively perceptually enhanced. Importantly, in such studies, participants tend to report that they were not aware of the perturbations between the movement and the consequences, suggesting that the signals for sensory discrepancies are not available to our conscious awareness.

This predictive process is also likely to be at the root of why physical fights always seem to escalate. Notice how tit-for-tat tussles between children tend to intensify, with each person claiming that the other hit him or her harder. In a recent study (Shergill et al., 2003) a motor was used to apply a brief force to the tip of each participant's left index finger. Participants were then asked to match the force they felt using their right index finger by pushing down on a force transducer attached to the motor. Results showed that participants consistently applied a stronger force than that which had been applied to them. The authors suggest that, just like when we try to tickle ourselves, the brain predicts the sensory consequences of the self-generated force and then reduces the sensory feedback. Since the forward model can only predict the outcome of our own actions and not of those of someone else, sensations that are externally caused are

enhanced relative to self-produced sensations. As a result, if you were to deliver a vengeful punch to match the force of your opponent's blow, it is likely that you would overestimate the strength of the opponent's punch and strike back harder.

1.7.10.4. Brain areas involved in maintaining awareness and making predictions

There is accumulating evidence that a cerebellar-parietal network is involved in predicting and attenuating self-produced, relative to externally produced sensations (Blakemore et al., 1998a; 1998b; 2001). In an fMRI experiment that employed the tickling paradigm described above, during externally produced touch, activity in the bilateral parietal operculum (the secondary somatosensory cortex) and ACC was higher than during the self-touch condition (Blakemore et al., 1998a). In addition, there was less activity in the right cerebellar cortex during a self-generated movement with a tactile consequence compared to an identical movement with no tactile consequence. A PET study revealed that activity in the right lateral cerebellar cortex increased as time delays between the onset of a self-generated movement and its sensory effect were increased. This suggests that this region is involved in signalling sensory discrepancies between predicted and actual sensory outcomes of motor acts (Blakemore et al., 1998b).

These data support other studies that implicate the cerebellum and PC in sensorimotor prediction. Electrophysiological studies show that neurons in the cerebellum are involved in reaching and grasping movements, firing before the onset of the action (Smith et al., 1993). They may therefore be involved in the rapid detection of errors during motor preparation and producing error signals at a sub-conscious level (Blakemore & Sirigu, 2003). Electrophysiological studies have also demonstrated that neurons in the PC are activated during planning of eye movements (Duhamel et al., 1992) as well as during reaching and grasping movements (Buneo et al., 2002).

Neuroimaging studies have revealed differential activation of the inferior PC for tasks involving action of the self versus action of another. For instance, this region is activated more when an external agent controls a movement compared with when the subject controls a movement themselves (Farrer & Frith, 2002). The inferior PC is activated when participants mentally simulate actions from someone else's perspective compared with they imagine performing the action themselves (Ruby & Decety, 2001), answer conceptual questions from a third person perspective compared with from their

own perspective (Ruby & Decety, 2003), and think about how another person would feel in certain situations relative to how they would feel (Ruby & Decety, 2004) (see Chapter 2). It has been argued that the cerebellum is involved in the rapid detection of discrepancies between actual and predicted sensory effects of movements, signalling errors below the level of awareness, while the PC is concerned with higher level prediction, such as the maintenance of goals, monitoring of intentions and the distinction between the self and others. This information may be available to conscious awareness (Blakemore & Sirigu, 2003).

1.8. Summary

Social cognition in humans is associated with a system that includes frontal, parietal and superior temporal cortex. A handful of studies have begun to investigate how development of these brain regions leads to development of social cognition. So far, these have focused on face emotion processing.

Action understanding is proposed to be a mechanism that enables social understanding. The MNS, sensitive to the observation of actions, sensations and emotions of others as well as the self, are found in some overlapping areas, particularly in FC and PC. MNS activity reflects the activation of action representations in the brain, which are crucial for both sharing the experience of others' actions and emotions, as well as for the distinction between the self and other, and the sense of authorship of action.

1.9. Objectives of the experimental studies in this thesis

In this review of social cognition and the MNS, I have attempted to describe the building blocks of social cognition in terms of TOM and its precursors and then to outline how motor cognition can be related to social information processing and therefore used as a way to study intersubjectivity. Throughout, I have mentioned the brain systems thought to be implicated in these cognitive processes, including, most importantly, FC, PC and STS. The first section in this chapter reviewed structural and functional brain imaging studies, to demonstrate that the brain areas undergoing the most profound development during adolescence overlap with those typically involved in self-other interactions. I have also described the results of behavioural studies during adolescent development, and have shown that most of the efforts have so far focused on the study of executive function development, while there is a dearth of data on social cognition during this period.

Given the correspondence between those areas that are developing in the adolescent brain with those areas involved in perspective taking and intention understanding, which, in turn, have some overlap with brain regions for action representation, the following studies aim to:

(i) measure social cognitive development, namely, perspective taking and intention understanding, during adolescence

(ii) measure development in action representation during adolescence using a variety of motor imagery tasks

(iii) use insights from psychopathology, in particular, autism and schizophrenia, in which self-other interaction is atypical, to delineate how the cognitive mechanisms of intersubjectivity might be subject to disruption.

The next chapter presents the first empirical study in this thesis, which investigates how the social cognitive skill of perspective taking develops during adolescence.

THINKING ABOUT HOW PEOPLE FEEL

CHAPTER 2

2. THE DEVELOPMENT OF PERSPECTIVE TAKING DURING ADOLESCENCE

2.1. Perspective taking in adolescence

Adolescence involves sexual maturity in terms of hormones and physical development of the body, and is also characterised by an increase in the complexity of group interactions and thus social behaviour (Lerner & Steinberg, 2004). Adolescence is a period of consolidation of the social self, that is, the development of identity and understanding of the self in relation to the social world (Coleman & Hendry, 1990). Anecdotal evidence and self-report data indicate that children seem to become progressively self-conscious and concerned with other people's opinions as they go through puberty and the period of adolescence (Berzonsky & Adams, 2003). The psychosocial context for adolescents is markedly different to that for children and adults. For example, relationships with peers, family and society go through distinct developments during this time. Adolescents begin to assert more autonomous control on their decisions, emotions and actions, disengaging from parental control for example (Coleman & Hendry, 1990). At the same time, the school context involves an intense socialisation process during which adolescents become increasingly aware of the perspectives of classmates, teachers and other societal influences (Berzonsky & Adams, 2003). This transitional period seems to involve both the establishment of a sense of self as well as a process of orienting towards others.

2.1.1. Increased awareness of others during adolescence

The emergence of the social self seems to be marked by a period of heightened self-consciousness, during which adolescents are thought to become preoccupied with other people's concerns about their own actions, thoughts and appearance. This development has been described in terms of phases of egocentrism during childhood and adolescence (Elkind, 1967). This account is based on Piaget's stages of cognitive growth (Inhelder & Piaget, 1958). It is proposed that after children develop internal representations of objects and referential thinking during early childhood, they reach the stage of the "emergence of concrete operations", and between the ages of seven and 11, they have acquired the mental tools to deal with classes and hierarchies. However, at this stage of

childhood, these abilities are restricted to concrete, physical entities and not abstract thought. Children of this age group therefore manifest "concrete operational egocentrism", or the inability to distinguish between a mental construction and perceptual phenomena. According to the Piagetian developmental account, by age 11, the emergence of "formal operational thought" enables children to differentiate between the perception of an object and their own mental construction of it, allowing them to objectify their own thoughts and reason about them. It is this form of thinking that allows children in early adolescence to conceptualise other people's thoughts and take their perspectives (Inhelder & Piaget, 1958).

Affective development during adolescence is thought to occur in synchrony with epistemological development (Benack, 1984). It is proposed that a change in knowledge of the world, and of the self and others in relation to the world enables a change in the knowledge of other people's mental states. Benack called this a shift from being a "dualist" to a being a "relativist". In this context, we might hypothesise that pre-adolescent children are dualists, such that they are able to distinguish between a person's experience and reality, but that any differences between experience and reality are considered deviations from an objective "truth". On the other hand, older adolescents and adults might be described as relativists who are able to view the nature of other people's experience through multiple frames of reference, taking into account subjective factors. For relativists, there is not necessarily a general truth; rather, validity is given to many different truths based on subjective factors. It is suggested that a shift in epistemological sequences might be linked to an improvement in empathy (Benack 1984). A shift towards relativistic thinking during adolescence might therefore increase the flexibility required to understand other people's perspectives and enhance the ability to maintain the distinction between the two perspectives and emotional states of the self and the other.

2.1.1.1. The imaginary audience

The development of adolescent egocentrism is thought to be a dialectic process: it is the ability to represent other people's thoughts as distinct from their own and therefore decentre themselves that also drives the new form of egocentrism. In other words, as soon as they are able to understand that other people have distinct thoughts and perspectives, they become preoccupied with the notion that other people's thoughts are

focused on their own behaviour or appearance (Elkind, 1967). Elkind's original theoretical model of adolescent egocentrism delineates two ideation patterns thought to arise as a consequence, and to characterise common adolescent social behaviours: the *imaginary audience* and the *personal fable*. The notion of the imaginary audience refers to adolescents' beliefs that others are watching and evaluating them, and that they are the object of other people's scrutiny. According to Elkind's theory, this belief results in an increased self-consciousness, a tendency to anticipate reactions of other people in relation to the self, and a feeling of being the focus of attention, regardless of whether a real audience exists or not in the situation. The personal fable, a related construct, denotes adolescents' convictions of their own personal uniqueness, giving rise to the sense of being 'special' (Elkind, 1967).

Since this original account of adolescent egocentrism, social psychological studies have investigated the imaginary audience with questionnaires and qualitative approaches. The exact age, validity and explanation (e.g. Bell & Bromnick, 2003; Frankenberger, 2000; Lapsely & Murphey, 1985; Vartanian & Powlishta, 2001) of Elkind's account of adolescent egocentrism have been challenged, and the theory has since evolved. Nevertheless, the number of reformulations and critiques of the original theory and the subsequent social psychological studies attest to the notion that social thinking during adolescence is marked by a focus on "what other people think".

2.2. Shifting from one's own viewpoint to another's viewpoint

2.2.1. What is perspective taking?

The ability to take another's perspective is crucial for successful social communication. In order to reason about others, and understand what they think, feel or believe, it is necessary to step into their 'mental shoes' and take their perspective (Gallese & Goldman, 1998). Perspective taking includes awareness of one's own subjective space or mental states ("first-person perspective", or 1PP) and requires the ability to ascribe viewpoints, mental states or emotions to another person ("third-person perspective" or 3PP). It is thus related to first-order TOM in that it involves surmising what another person is thinking or feeling (Harris, 1989). It requires the ability to distinguish the self from someone else and appreciate another's intentions or beliefs. The ability to adopt another's viewpoint may underpin the ability to read other minds and understand

another's feelings (Humphrey, 1976).

However, a distinction between cognitive perspective taking and empathy is required here. A recent definition proposes that there is empathy if "(i) one is in an affective state; (ii) this state is isomorphic to another person's affective state; (iii) this state is elicited by the observation of imagination of another person's affective state; (iv) one knows that the other person is the source of one's own affective state" (de Vignemont & Singer, 2006, pp. 435). Thus empathy, like perspective taking, requires the ability to understand another person's emotions but the ability to distinguish between the self and other. Perspective taking, however, does not meet the first condition outlined above. In other words, to understand how one might feel, or how another person might feel, in given scenarios, it is necessary to represent mental states of other people but it is not necessary to be emotionally involved, oneself (de Vignemont & Singer, 2006). For example, it is possible to attribute fear to another person, based on one's knowledge of that person or the understanding of their behaviour in a threatening scenario, but it is not necessary to *feel* the fear.

2.2.2. Frames of reference and role taking

Current literature on perspective taking subsumes different forms of processing. It is therefore worth noting the distinction between the phenomenal and representational levels of self-other relationships. As detailed by Frith and de Vignemont (2005) and Vogeley and colleagues (2004), one can take different perspectives in terms of spatial representations, such that the locations of other entities in space are represented by the beholder in different reference frames. In an egocentric frame of reference, the location of an object is represented in relation to the subject, i.e., in relation to the personal agent (e.g. is the line on your right or left?), whereas in the allocentric frame of reference, the location of one object in relation to another object is represented by the agent (e.g. is the line on the right or left of the square?). Thus, while the egocentric perspective relates that which is seen to the agent who sees it, the allocentric perspective is independent of the agent's position.

At the phenomenal level, however, the first-person perspective (1PP) (e.g. is the line on your right or left?) and the third-person perspective (3PP) (e.g. is the line on his right or

left?) are both centred on an agent. Crucially, perspective taking at this phenomenal level requires "the translocation of the egocentric viewpoint" from the 1PP to the 3PP (Vogeley & Fink, 2003). Thus, emotional perspective taking, analogous to role taking, for example, considering how "I" would feel versus how "she" would feel, necessitates a shift in the egocentric perspective.

2.3. Mechanisms of perspective taking

There is currently much debate surrounding the mechanism of perspective taking. How do we automatically switch roles from the self to the other in everyday social interactions? One prevalent view is that we understand others by mentally simulating their actions (Goldman, 1989; Harris, 1995). In support of this "simulation theory", a growing body of evidence from neurophysiological studies has demonstrated that common brain areas are activated both when we execute an action and when we observe another person perform the same action (Buccino et al., 2001; Decety et al., 1997; Grafton et al., 1996; Rizzolatti et al., 1996a; Rizzolatti et al., 1996b). Simulation theorists draw on the existence of a MNS to suggest that simulating other people's actions is an ontogenic precursor to understanding their thoughts and emotions (Gallese & Goldman 1998). On the other side of the debate is "theory theory", or the idea that we use a common sense psychological theory, or "folk psychology" to understand other minds, rather than internally simulating them (e.g. Gopnik & Meltzoff, 1997).

2.4. Perspective taking and the brain

The brain regions that undergo the most significant development during adolescence overlap with those that have been linked to the ability to take other people's perspectives. Functional neuroimaging studies have revealed that frontal, parietal and superior temporal cortex are associated with making the distinction between 3PP and 1PP at the motor (Ruby & Decety, 2001), visuo-spatial (Vogeley et al., 2004), conceptual (Ruby & Decety, 2003; Vogeley et al., 2001) and emotional (Ruby & Decety, 2004) level. While these have shown common activations in prefrontal and parietal areas (Vogeley et al., 2004) as well as SMA, precentral gyrus, precuneus, MT/V5 (Ruby & Decety, 2001) and common deactivations in areas such as lateral

superior temporal cortex (Vogeley et al., 2004), differential activity between the two perspective conditions has also been reported.

The series of studies by Ruby and Decety of emotional (2004) and conceptual (2003) perspective taking show that thinking about how another person, such as your mother versus you, would feel, or what a medical student versus you would think, are associated with increased activity in medial superior frontal gyrus, left STS, left temporal pole and right IPL, while for shifting perspectives in their motor imagery task (2001), the same contrast of 3PP versus 1PP elicited increased activity in similar areas including right IPL and frontopolar gyrus. suggesting continuity of cognitive and neural processes between motor, conceptual and social emotional processes in perspective taking tasks. In addition, neuroimaging and TMS studies have implicated the inferior PFC in the distinction between self and others at the sensorimotor level (Farrer & Frith, 2002). In line with simulation theory, therefore, some common neural networks are recruited for taking the 1PP and 3PP. However, as Vogeley and colleagues (2001) indicate, the differential brain activity suggests that simulation cannot be the only mechanism since distinct brain regions are also activated, presumably to monitor who the agent is in the interaction.

Furthermore, MPFC plays a role in differentiating between the self and a familiar but unknown other such as George W. Bush (Kelley et al., 2002) and between the self and a personally known other such as a close friend (Heatherton et al., 2006). Neuroimaging studies continue to associate MPFC with mentalising tasks (cf. Amodio & Frith, 2006). For example, the attribution of mental states to abstract moving triangles in animations activates MPFC, as does playing interactive games that require mutual cooperation between players (McCabe et al., 2001). In another neuroimaging study investigating TOM processes, MPFC and STS were activated when participants were required to surmise what another person from another era (Christopher Columbus) would know about the use of certain tools (Goel et al., 1995). Thus thinking about other people has consistently been associated with MPFC, through functional neuroimaging paradigms (see Introduction, Chapter 1 for more details of paradigms).

Recently, using fMRI, Aichhorn and colleagues (2006) investigated whether, like social perspective taking and TOM tasks, visual perspective taking is associated with MPFC

activity in adults. They developed a paradigm that strictly necessitated a shift of perspective in a computerised visuo-spatial task. The results demonstrated that MPFC was not involved in visual perspective taking, but that posterior regions of the STS and the TPJ were involved in judging what another can see. These results echo findings from TOM studies, which also require a shift in perspective (see Frith & Frith, 2006, and Introduction, Chapter 1). Drawing on results of differential neural networks shown to be involved in visual compared with social perspective taking in various studies, Aichhorn and colleagues suggested that different aspects of TOM are required in different types of perspective taking. They suggest that the dorsal posterior STS/TPJ region is involved in realising that minds represent the world differently and representing "cold" facts about the mind, that include perspective distinctions and behavioural predictions. On the other hand, they propose that MPFC is involved in representing "hot" information such as predicting the emotional consequences of behaviour (Aichhorn et al., 2006).

The studies on mentalising and perspective taking described above have involved adult participants. None, so far, has investigated the development of these skills during adolescence. Given the demands of the social environment in adolescence, and the development of the brain areas associated with mentalising, components of mentalising might be expected to develop during this period.

2.5. Experiment 1: Development of perspective taking during adolescence

2.5.1. Introduction

Studies have focussed mainly on the development of executive functions during adolescence and have shown that a variety of executive functions improve with age during adolescence (e.g. Anderson et al., 2001). Aside from a handful of studies on recognition of facial expressions (Killgore et al. 2001; Monk et al., 2003; Nelson et al., 2005), there has been a lack of attention on the development of social cognition during this time period. In the field of social cognitive development, so far, much attention has been devoted to the development of TOM during childhood (e.g. Wimmer & Perner, 1983), as well as to the consequences of its delay or impairment (e.g. Baron-Cohen et al., 1985). Since Piaget's studies using the "three mountain problem" (Piaget &

Inhelder, 1948/1956), only a handful of social psychology studies have investigated perspective taking in early to mid childhood (e.g. Bosacki & Astington, 1999) and to our knowledge, none has considered its development during adolescence. As well as changes in behavioural development, the transition from childhood to adolescence is marked by dramatic structural changes in the brain (Paus, 2005). MRI studies have shown a reduction in GM volume, which is most prolonged in FC, PC and STS. There is a simultaneous increase in WM volume, according to these MRI data. These changes correlate with the decreases in synaptic density and increases in myelinated axons found in earlier post-mortem investigations (Huttenlocher et al., 1983; Huttenlocher & Dhabolkar, 1997; Yakovlev & Lecours, 1967). Taken together, these structural changes have been taken to reflect the processes of synaptic pruning and myelination during adolescence (Giedd et al., 1999a; Gogtay et al., 2004; Sowell et al., 2003; Toga et al., 2006).

The brain regions that undergo the most significant development during adolescence are also those that have been linked to the ability to take other people's perspectives. Studies have shown that TOM develops in infancy by the age of five (Barresi & Moore, 1996; Leslie, 1994). So, what are the cognitive consequences of the continued development of its underlying neural circuitry? Clearly, development of associated abilities is going to be subtle. Given that the social environment dramatically changes during adolescence, and that the brain undergoes a restructuring process, it might be expected that social cognitive abilities such as perspective taking develop during adolescence.

Taking a cognitive neuroscience approach, the development of perspective taking before, during and after adolescence was investigated[4]. Perspective taking was in the emotional domain, such that participants were required to consider their own response to certain emotional situations or those of another person. The processing of first-person and third-person emotional perspectives were contrasted. Given the reorganisation of PFC and PC that takes place around puberty, it was predicted that perspective taking becomes increasingly efficient during adolescence. This hypothesis would predict that

[4] See Choudhury, S., Blakemore, S.-J & Charman, T. Social cognitive development during adolescence. *Social Cognitive & Affective Neuroscience,* in press

the difference in RT between 3PP and 1PP (Δ RT) would progressively decrease with age.

2.5.2. Method

2.5.2.1. Participants

112 participants were recruited: 33 pre-adolescent children (12 males, 19 females; mean age 8.6 years, SD=0.46), 41 adolescents (20 males, 21 females; mean age 12.9 years, SD=1.20) and 38 adults (20 males, 18 females; mean age 24.0 years, SD=4.05). Child participants were from a state comprehensive primary and secondary schools in the London area and adults were students at University College London. Participants were screened to ensure that they were right handed and that none had a history of psychiatric, neurological, developmental or learning disorder. Written informed consent was obtained from the participants and, for children, from their parents prior to the study, which was approved by the local ethics committee.

2.5.2.2. Experimental design

Participants were presented with a series of written scenarios. First, a one-line sentence describing an everyday scenario was presented on a laptop computer screen together with a question concerning how the participant himself or herself (for 1PP scenarios), or how the protagonist (for 3PP scenarios), would feel in such circumstances (Figure 2.1). There were 120 trials altogether, of which half conveyed the question in the first person ("How do you feel?") and the other half asked the same question but about a hypothetical character in the third person ("How does he/she feel?"). The participant was instructed to press the space bar after reading the question at his or her own pace. This elicited the presentation of two possible response choices in the form of simple cartoon faces, each representing one of five possible emotions: very happy, happy, neutral, sad, afraid and angry. The participant was asked to choose one of the two possible faces in answer to each question, as quickly as possible. As soon as the participant responded, the next scenario appeared. Reaction times (RT), taken as the time in milliseconds (ms) between the presentation of the answer screen and the key press for the chosen answer, were recorded by the computer.

Perspective. Scenarios either concerned 1PP or 3PP:

First-person perspective (1PP): Questions focussed on what emotion the participant would feel given a particular social situation. For example: 'You have had an argument with your best friend. How do you feel?' These questions were designed to require the participant to think about his or her own emotional response in certain contexts.

Third-person perspective (3PP): The same questions involving exactly the same scenarios were asked, only the situation described involved a hypothetical other person and the question was conveyed in the third person. For example: 'A girl has had an argument with her best friend. How does she feel?' These questions were designed to require participants to think about another person's likely emotional response in equivalent contexts to the 1PP condition. See Figure 2.1 and Appendix 2.

Choice type. The trials were designed to be of two types: Open and Closed. This created two levels of difficulty, the rationale being that any RT difference between the 1PP and 3PP conditions might be more apparent in the open condition, since the answer choices for these questions were designed to be more ambiguous and require more thought.

Open (O): In the open answer trials, both faces on the answer screen were designed to be equally appropriate responses to the emotional situation outlined in the preceding question screen, e.g. sad and angry. See Figure 2.1.

Closed (C): In the closed trials, one of the two choices of faces was designed to be clearly a more appropriate response to the emotional situation outlined in the preceding question screen, e.g. happy and sad. See Figure 2.1.

The number of characters and clauses in each scenario were matched between conditions.

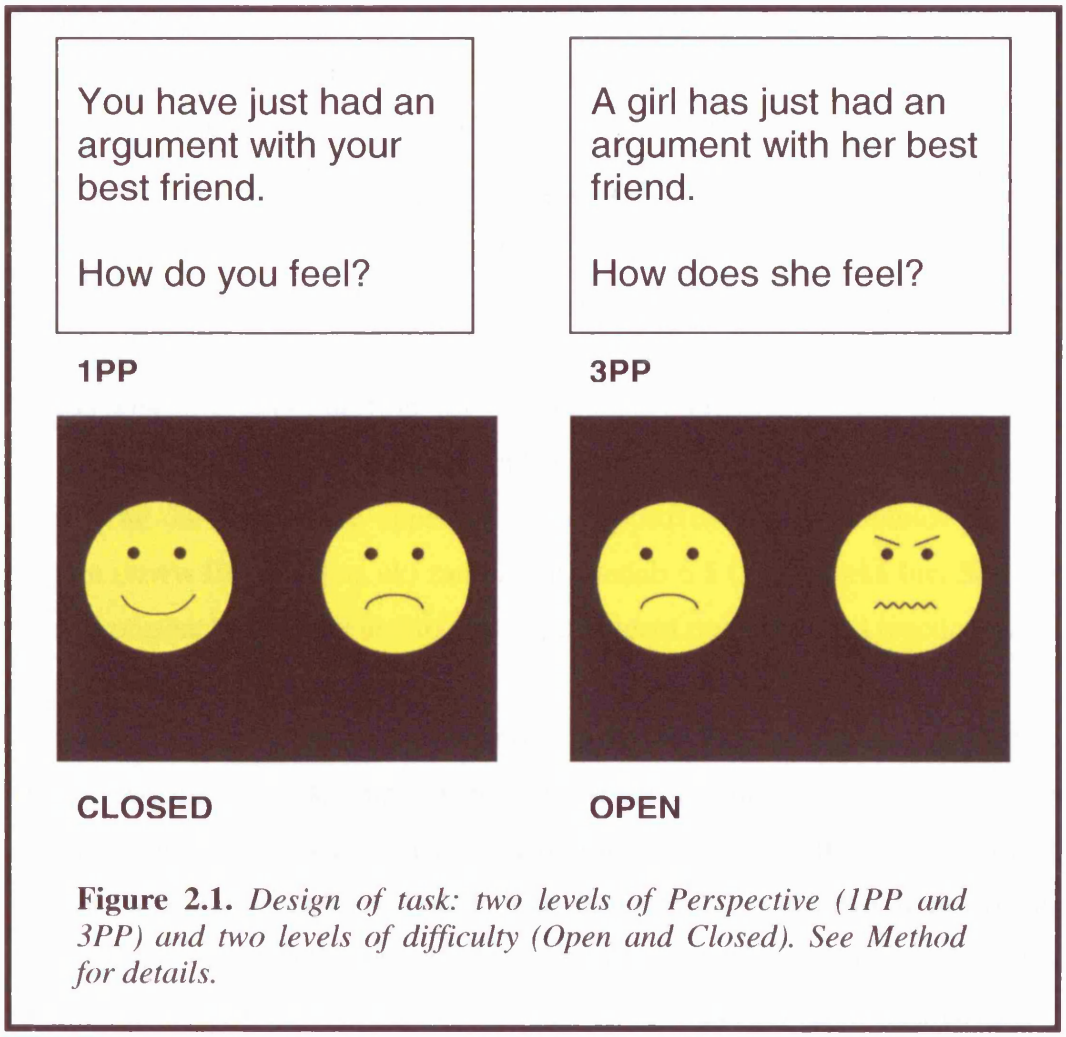

Figure 2.1. *Design of task: two levels of Perspective (1PP and 3PP) and two levels of difficulty (Open and Closed). See Method for details.*

2.5.2.3. Experimental procedure

Stimulus presentation. The questions were delivered in four blocks of 30 question and answer stimuli, in a pseudorandom order that was counterbalanced between the participants. It was ensured that each of the Perspective and Choice Type conditions were equally represented in each block. Stimuli within each block were presented in a random order and each question occurred only once in each block. There was a rest period between the blocks and participants were told that they could continue with the task when ready, by pressing the space bar. To indicate their response, participants were instructed to use the right hand and to press either the F or the H key (chosen for their central position on the keyboard) to indicate their answer. These keys were colour-coded and participants were instructed to press the key that corresponded to the side of the screen of their selected answer face. As soon as the participant had pressed an answer key, the next question was automatically presented. Each block of questions lasted approximately two minutes and testing was conducted individually in a quiet room. The duration of the experiment was approximately 10 minutes per participant. Cogent (www.fil.ion.ucl.ac.uk) running in Matlab 6.5 (Mathworks Inc, Sherborne) was used to present the stimuli and to record participant responses and reaction times.

Instructions. Each participant was shown a Powerpoint presentation which explained how to perform the task, emphasising that the participant should pay careful attention to the person whose perspective they were required to take, and that they should choose an answer as quickly as they could. The presentation was also used to check that participants understood the emotions represented by each of the faces. Participants were then given a practise condition consisting of six example questions (which were not included in the main experiment).

2.5.2.4. Data analysis

Reaction time

For each participant, median RTs were calculated for each of the four conditions of 1PPO, 1PPC, 3PPO and 3PPC, and for 1PP and 3PP overall, irrespective of Choice Type. The difference between the median RT for 1PP and 3PP was then calculated for each participant (Δ RT). Data were analysed using a univariate ANOVA to test the effects of age and gender on Δ RT.

Error analysis

Since the response choices in the Open condition were entirely subjective and purposely ambiguous, there was no correct answer, only the timing of responses was used in the analyses. In the Closed condition, there was a more obvious correct answer and an obvious incorrect answer. An error analysis was therefore performed for all subjects in the Closed condition. The correct answer was determined beforehand, and each subject's answers to Closed condition questions were "marked" for errors. A percentage error was given to each subject, for each of the 1PP Closed and 3PP Closed condition. A 2 x 3 repeated measures ANOVA (2 levels of perspective: 1PP % error, 3PP % error; 3 levels of age: pre-adolescent, adolescent, adult) was used to test the hypothesis that difference in percentage (%) error between 1PP and 3PP becomes less pronounced with increasing age. In other words, an interaction was predicted between errors in each Perspective condition and age.

2.5.3. Results

All participants were able to follow the instructions and perform the tasks. Two outliers were excluded because their median RT for one of the perspective conditions fell below 3SD of their group mean.

2.5.3.1. Reaction time analysis

A univariate ANOVA was performed to investigate the effect of Age (three levels: preadolescence; adolescence; adult) and Gender (two levels: male; female) on the non-directional differences in RT between 1PP and 3PP (collapsed across Open and Closed conditions). There was a main effect of age group showing that Δ RT decreased significantly with age ($F(2,104) = 10.82$; $p<.0001$; see Table 2-1). Post-hoc Bonferroni tests indicated that the mean Δ RT was significantly larger in pre-adolescents compared with adults ($p<0.0001$) and in adolescents compared with adults ($p<0.005$). Mean Δ RT was not significantly different in pre-adolescents compared with adolescents (see Table 2-1 for RTs in ms for the three groups of subjects in each condition (3PP and 1PP), and the difference in RT between conditions). This relationship between age and Δ RT can also be seen in Figure 2.2, showing a correlation between Δ RT and age in years. This graph shows that there is a significant negative correlation between age and Δ RT ($R^2 = 0.145$ ($p<0.01$)).

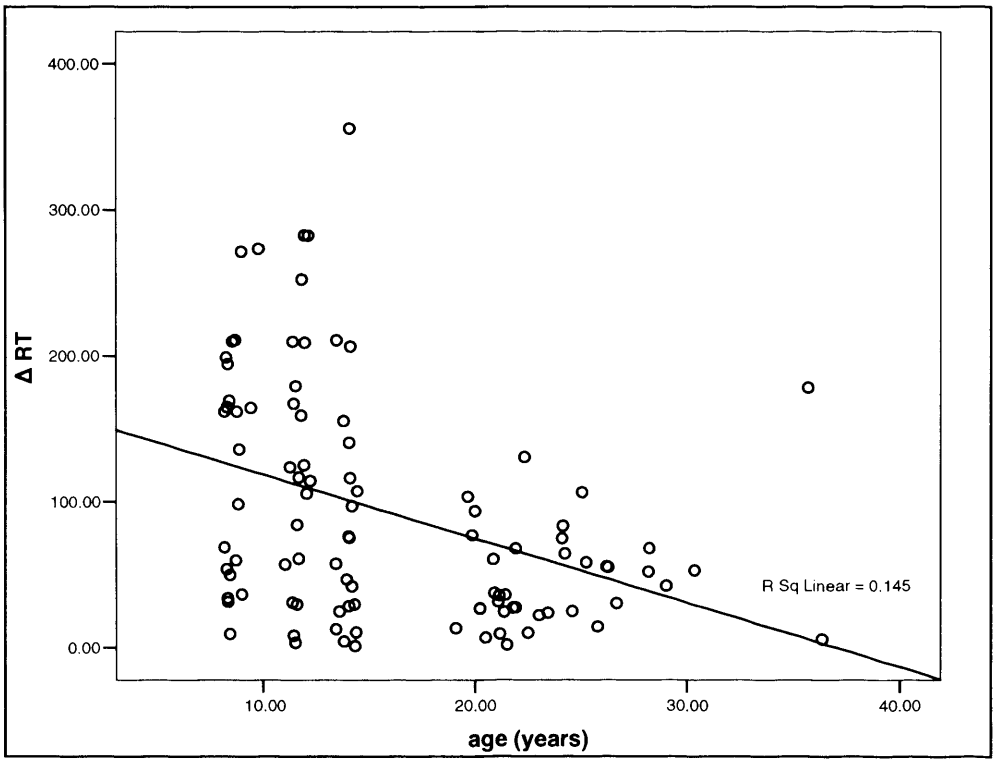

Figure 2.2. ***Relationship between Δ RT and age.*** *This graph shows that there is a significant negative correlation between age and Δ RT (R^2 = 0.145 ($p<0.01$)*

	Mean±SE RT (ms) in 3PP	**Mean±SE (ms) RT in 1PP**	**Mean±SE (ms) Δ RT**
Preadolescent (N=31) (mean age 8.6)	1739.7 ± 74.1	1712.7 ± 69.1	143.6 ± 19.5
Adolescent (N=41) (mean age 12.9)	1248.5 ± 45.9	1199.1 ± 43.7	112.1 ± 13.9
Adult (N=38) (mean age 24.0)	903.5 ± 35.1	894.0 ± 35.4	48.6 ± 6.2

Table 2-1 *Mean reaction times and non-directional Δ RT (3PP-1PP) for each perspective condition for every age group.*

The effect of age on Δ RT was consistent within the Open (Δ RT-O) and Closed (Δ RT-C) conditions, as well (Figure 2.3). A univariate ANOVA showed that there was a significant effect of age on Δ RT-O ($F(2,104)=5.2$; $p<0.05$). Post-hoc t-tests indicated that in this condition, there was a significant difference between pre-adolescents and adults ($p<0.05$). Similarly, Δ RT-C significantly decreased with age ($F(2,104)=6.9$; $p<0.005$), and again, post-hoc t-tests showed that Δ RT-C was significantly higher for pre-adolescents than adults ($p<0.001$).

Δ RT (collapsed across Open and Closed conditions) was plotted to investigate directionality (see Figure 2.4). As shown in the graph, ΔRT among both groups of younger participants was larger and spread almost equally in both directions (i.e. 3PP>1PP and 1PP>3PP) whereas among adults there was little difference with Δ RT values clustering around the zero mark of the difference scale (i.e. 3PP = 1PP). The difference was most pronounced for the pre-adolescent group, less so for the adolescents and negligible for the adults.

There was no significant effect of Gender on Δ RT ($F(1,104)=1.69$; $p=0.17$), nor was there a significant effect interaction between Age and Gender ($F(2,104)=0.717$; $p=0.49$).

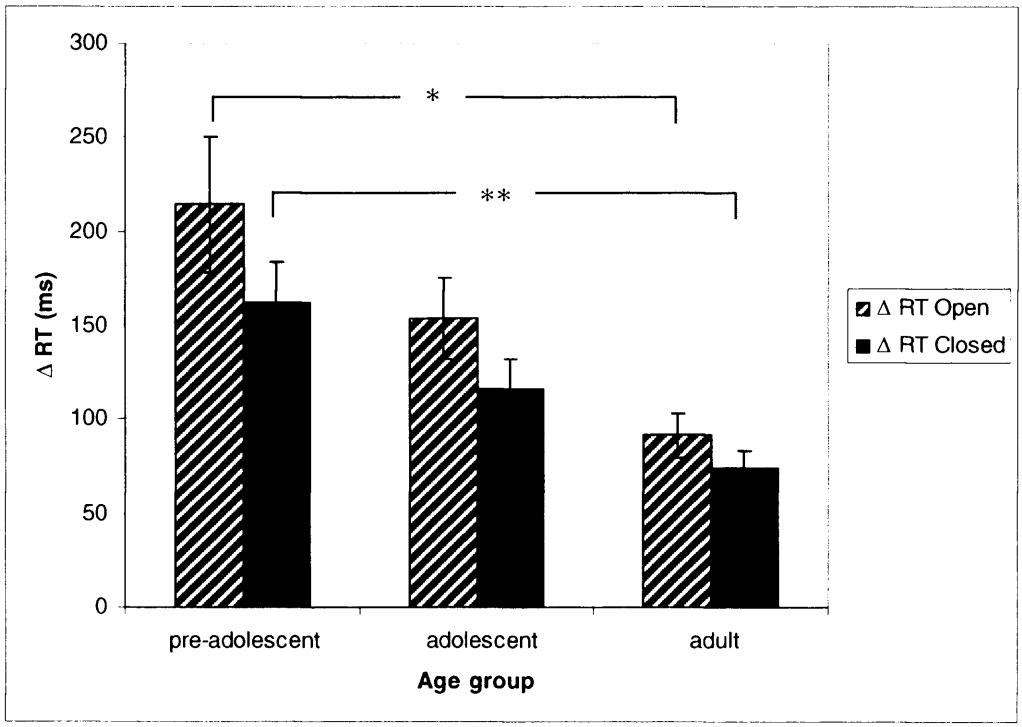

Figure 2.3. **Δ *RT for each Choice Type*** *condition for each age group, showing that Δ RT decreases with age in both the Open and Closed conditions, with pre-adolescents having a significantly higher Δ RT in both Choice Type conditions than adults. *p=<0.05; **p=<0.001.*

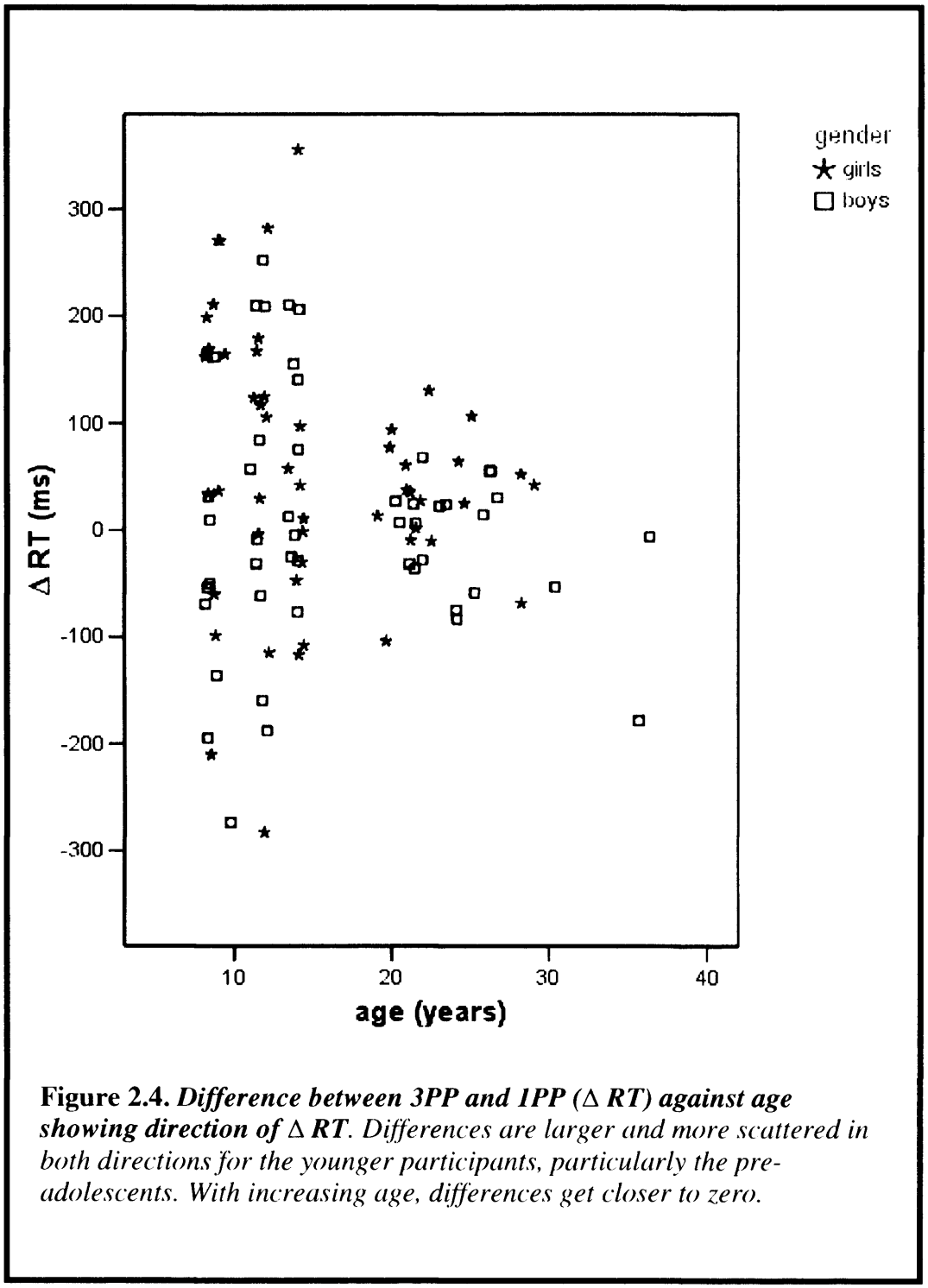

Figure 2.4. ***Difference between 3PP and 1PP (Δ RT) against age showing direction of Δ RT.*** *Differences are larger and more scattered in both directions for the younger participants, particularly the pre-adolescents. With increasing age, differences get closer to zero.*

2.5.3.2. Error analysis

There was a main effect of age group ($F(2,105)=5.9$, $p<0.005$) indicating that the % errors overall decreased with increasing age (% error ± S.E.(pre-adolescents)=7.5±0.87; (adolescents)=4.3±0.69; (adults)=4.0±0.46) (Figure 2.5). Post-hoc Bonferroni-corrected t-tests indicated that pre-adolescents made significantly more error across both perspective conditions, compared with both adolescents ($p<0.05$) and adults ($p<0.005$). There was no significant difference in the overall percentage error between adolescents and adults (Figure 2.5). However, there was no effect of Perspective condition on the number of errors ($F=(1,105)=0.20$, $p=0.66$) nor an interaction between Perspective condition and age ($F=(2,105)=1.2$, $p=0.30$).

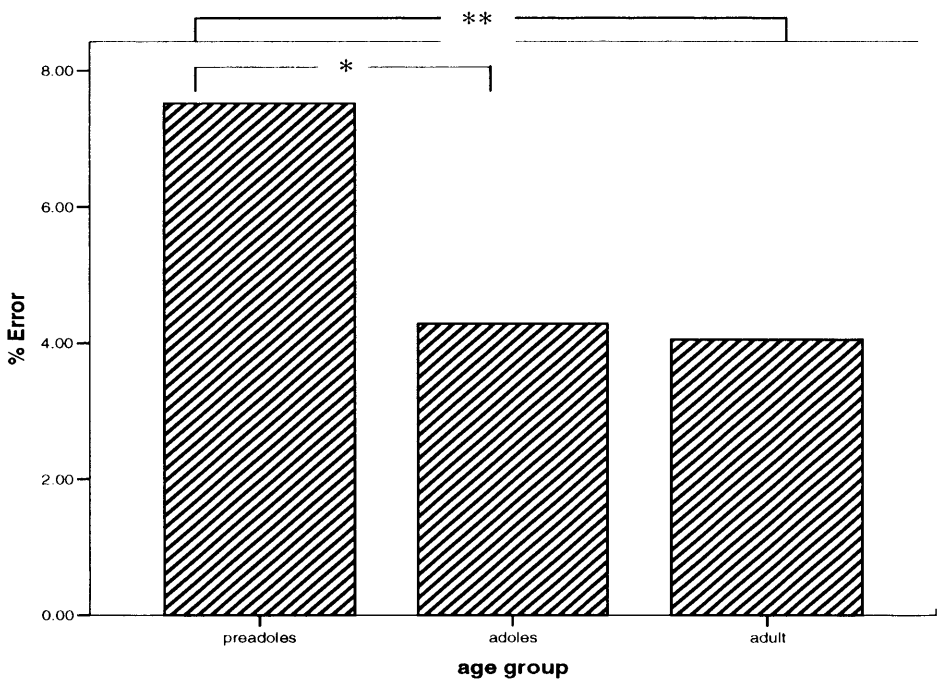

Figure 2.5. ***Error analysis***. *Pre-adolescents made significantly more errors than adolescents and adults, from both perspectives in the Closed condition *p=<0.05; **p<0.005*

2.5.4. Discussion

In this study, the development of perspective taking during adolescence was investigated. A novel perspective taking task was designed, suitable for a large age range spanning middle childhood, adolescence and adulthood. The difference in RT between 3PP and 1PP conditions (Δ RT) significantly decreased with increasing age between late childhood and adulthood. Whilst Δ RT was relatively large among pre-adolescents, it became progressively smaller with age. The spread of Δ RT was both in the positive (3PP>1PP) and negative (1PP>3PP) directions among the pre-adolescent children whereas the RT for 1PP and 3PP conditions was more or less equal for adults. In line with our prediction, this finding suggests that the efficiency and possibly the strategy of perspective taking develops during adolescence, in parallel with the maturation of neural networks subserving social cognitive processes during adolescence. The relatively higher proportion of errors in the Closed condition among the pre-adolescents may indicate that the less systematic response style of the pre-adolescents, compared with the two older groups is also associated with greater difficulty (less accuracy) in perspective taking.

2.5.4.1. Inefficient perspective taking among pre-adolescents

According to Piaget's stages of cognitive growth (Inhelder & Piaget, 1958), the pre-adolescent group, aged around nine years, is able to carry out formal operational thought, which includes being able to conceptualise other people's thoughts as distinct from one's own. Indeed, studies of the development of TOM have shown that children aged four are able to predict other people's intentions and emotional reactions (Harris, 1989; Wellman, 1990). By age nine, children should therefore be capable of taking into account the third person perspective. However, our results suggest that prior to adolescence, children have a less systematic processing strategy. The pre-adolescent group showed no systematic direction of difference between 1PP and 3PP, such that around half of the pre-adolescents took longer to take the 1PP (1PP>3PP), while the rest took longer to take the 3PP (3PP>1PP). It might be speculated, therefore, that prior to adolescence, the unsystematic direction of Δ RT reflects an immature cognitive mechanism for perspective taking. Whether this response pattern among pre-adolescents is a result of a relative difficulty in differentiating between the first- and third-person, or that children of this age group are less inclined, or find it more difficult, to enter into another person's "mental shoes", requires further investigation. The error

analysis (which was only applicable to the Closed conditions) demonstrated significantly more errors among pre-adolescents compared to adults. This suggests that pre-adolescents were not only less efficient but also more error prone than the older participants.

2.5.4.2. Neural and cognitive mechanisms of perspective taking

It has been suggested that we understand others by mentally simulating their actions and thoughts (Gallese & Goldman, 1998; Harris, 1995). In support of this "simulation theory", evidence has accumulated to show that common brain areas are activated when participants perceive a visual scene or answer a conceptual question from their own, first-person, perspective and from another person's perspective (e.g. Vogeley et al., 2004). In addition to simulating another person, it is also necessary to distinguish between the first- (self) and third- person (other), which is thought to activate PC (Farrer & Frith, 2002; Ruby & Decety, 2001). The synaptic reorganisation in FC and PC during adolescence is likely to have implications for social cognitive processes that depend on these brain regions. This conjecture is supported by the current results. If we assume that, among the age groups tested, adults are most experienced in social interaction and have mature frontal and parietal neural circuitry, then a low difference in Δ RT (3PP=1PP) is likely to indicate the highest proficiency in perspective taking. In contrast, the most pronounced difference in RT between 1PP and 3PP, seen in the pre-adolescent group, would therefore indicate relatively inefficient processing.

2.5.4.3. Cellular maturation in the frontal and parietal cortices during adolescence

There is accumulating evidence that the brain regions consistently involved in social interaction with other people, including PFC and PC (Frith & Frith, 1999; Gallagher et al., 2000; Ruby & Decety, 2001; 2003; 2004), are subject to structural development during adolescence. Post-mortem cellular studies have shown that there is a proliferation of synapses in the subgranular layers of the PFC during childhood followed by a plateau phase and a subsequent elimination of synaptic connections after puberty and throughout adolescence (Huttenlocher, 1979). In addition to this synaptic development, axons in PFC are myelinated from childhood to adulthood (Yakovlev & Lecours, 1967).

MRI studies have shown a peak of frontal and parietal GM just before puberty, from age seven to roughly 12, and a progressive net decline thereafter well into adulthood, along with a concomitant linear net increase in WM (Giedd et al., 1999a; Gogtay et al., 2004; Sowell et al., 2003). The peak in GM density just before puberty, followed by the decrease in grey matter density in frontal and parietal regions throughout adolescence has been interpreted as reflecting a wave of synaptogenesis at puberty followed by synaptic pruning (Giedd et al., 1999a; Gogtay et al., 2004; Huttenlocher, 1979, Huttenlocher et al., 1983; Sowell et al., 2003; Yakovlev & Lecours, 1967). There have been few empirical studies investigating social cognition during adolescence. Results from studies that have investigated development of executive function have shown development of selective inhibition, working memory and risk assessment. Improvement in performance was attributed to the ongoing myelination of the frontal lobes during childhood and adolescence (see Blakemore & Choudhury, 2006a for a review).

2.5.4.4. Synaptic pruning improves efficiency during adolescence

It is possible that children use different strategies for perspective taking and only gradually during adolescence does a unified, efficient strategy become refined. This refinement of performance may be conferred by the cellular changes occurring in the FC and PC during adolescence (Giedd et al., 1999; Gogtay et al., 2004; Huttenlocher, 1979, Huttenlocher et al., 1983; Sowell et al., 2003, Yakovlev & Lecours, 1967). It is possible that the net increase in GM thought to represent exuberant synaptic connections in frontal and parietal areas may account for the increased Δ RT of pre-adolescent participants. During adolescence, pruning of excess synapses, along with accelerated axonal conduction conferred by the myelination process, is proposed to lead to the consolidation of functional circuits in frontal and parietal areas (Giedd et al., 1999a), rendering cognitive processing more efficient (McGivern et al., 2002). Consequently, adults may have sufficiently fine-tuned neural circuitry to take the perspective of another person as efficiently as taking the first person perspective.

The differences between age groups are also likely to be influenced by differences in social experience. Compared to children and adolescents, adults are generally more skilled in instinctively inferring the perspectives of other people. Perhaps as a result of their mature neural circuitry supporting social cognition, as well as their greater social

experience, adults show no difference between RTs for 1PP and 3PP. Perspective taking in adults, in other words, is automatic.

2.5.4.5. Development of the strategy for perspective taking

While PC is involved in differentiating self and other, it has been proposed that STS is associated with the *prediction of actions based on past actions*, and that MPFC is involved in anticipating *future consequences of actions based on internal mental states* (Frith, *in press*). We know from executive function studies, that the ability to suppress impulses develops during adolescence, perhaps in line with PFC maturation (Adleman et al., 2002; Casey et al., 1997; Rubia et al., 2001; Tamm et al., 2002). As the ability to inhibit one's own impulses develops, and the ability to understand other people's mental states is refined, a change in the strategy of perspective taking might take place. Perhaps children and young adolescents have relatively poor inhibition of their own egocentric bias, and therefore rely on predicting other people's emotional perspectives based on the consequences of their *own past actions*. Maturation of PFC circuitry might facilitate a strategic shift such that older adolescents and adults can predict the feelings of other people based on how they *anticipate the other person would feel* if s/he were to make the action in the given scenario. Development of IPL might enable older adolescents and adults to keep the self/other distinction intact, while in pre-adolescents, immature circuitry in the area might lead to a blurring between 1PP and 3PP and the imposition of the self-perspective onto the other.

2.5.5. Conclusion

The significant decrease in the difference between RTs for 1PP and 3PP during adolescence found in the current study may reflect cognitive and behavioural features both experimentally (Steinberg, 2005) and anecdotally associated with adolescent development (see *Time Magazine*, June 7 2004). While several studies have investigated development of executive function during childhood and adolescence (Anderson et al., 2001; Casey et al., 1997; Luna et al., 2001; McGivern et al., 2002; Tamm et al., 2002), no empirical study to our knowledge has explored the development of social cognitive abilities during this time period. Perspective taking is a cognitive mechanism that underlies everyday social interaction. These data suggest that prior to adolescence, children are less efficient and have a less systematic and more error-prone style of processing the emotional perspectives of other people. During adolescence, social and

neural maturation occur so that by adulthood the cognitive processing for perspective taking is fast and systematic. Future fMRI studies are necessary to test our prediction that this reflects a developmental shift in the neural strategy required for perspective taking. The results from this novel perspective taking task appear to model the course of social behavioural development and provide an interesting basis for further research.

The next chapter investigates how the pattern of perspective taking differs between healthy adults and adult patients with positive symptoms of schizophrenia.

CHAPTER 3

3. PERSPECTIVE TAKING IN PATIENTS WITH POSITIVE SYMPTOMS OF SCHIZOPHRENIA

3.1. Schizophrenia

Schizophrenia is characterised by both negative and positive symptoms. Negative symptoms reflect a *lack* of typical behavioural features, and include apathy and emotional bluntness. Positive symptoms are features that are *present* in schizophrenia but not in healthy individuals. These include thought insertion, delusions of control, delusions of persecution and auditory hallucinations (see Table 3-1; DSM IV-TR, APA, 2000). Here, the focus is on persecutory delusions, which are a type of positive symptom in which a person holds a bizarre and paranoid belief with extraordinary conviction (Johnstone, 1991; Kraeplin, 1919; Ndetei & Vadher, 1984). Specifically, this study investigates perspective taking in patients with positive symptoms which were predominantly delusions of persecution. The next section describes delusions and outlines theories that have been proposed to explain them.

3.2. Delusions

Delusions, once described as the 'basic characteristics of madness' (Jaspers, 1963), are a key symptom of psychosis and are commonly associated with the diagnosis of schizophrenia. Like auditory hallucinations (which are the experiences of hearing speech or voices in the mind), delusions are experiences involving distortions of reality but that make sense to the believer. While delusions were traditionally considered to be resistant to change despite experiences to the contrary and counter-arguments (Johnstone, 1991; Kraeplin, 1919; Ndetei & Vadher, 1984;), it has recently been argued that delusional conviction changes over time and can be reduced by cognitive intervention, and is therefore better conceptualised as a dimensional rather than categorical phenomenon (Blackwood et al., 2001). Delusional beliefs are thus viewed as an extreme form of the normal belief system. The table below illustrates the diverse types of delusions exhibited by patients with schizophrenia (Table 3-1).

THEME	EXAMPLE
Defined by DSM	
Persecutory	"My food is being poisoned by the police"
Grandiose	"I have the power to heal all illnesses"
Jealous (Othello syndrome)	"My partner is cheating on me"
Erotomanic (De Clerambault's syndrome)	"A famous pop star secretly signals her love to me over the radio"
Somatic (e.g. delusional parasitosis/Ekbom's syndrome)	"I am infected by tiny parasites"
Bizarre	"My mother's thoughts are being carried on raindrops that fall on the air conditioner"
Misidentification	
Capgrass syndrome	"My relatives have been replaced by identical looking impostors"
Fregoli syndrome	"The same person is disguising himself as others"
Reduplicative paramnesia	"My present location exists in two places simultaneously"
Mirrored self-misidentification	"The reflection in the mirror is another person"
Other	
Thought insertion/withdrawal	"Thoughts are being inserted into/withdrawn from my mind"
External control	"My mind/body is being controlled by an external agent"
Guilt	"I am responsible for the AIDS epidemic"
Religious	"I am the reincarnation of Solomon"
Cotard delusion	"I am dead/do not exist" or "My body is decaying"
Lycanthropy	"I am/have transformed into an animal"

Table 3-1. *Examples of positive symptoms as defined by DSM-IV (adapted from Bell et al., 2006)*

Studies have indicated that delusional behaviour is associated with particular styles of cognition (Bell et al., 2006). For example, in the domain of probabilistic reasoning, delusional individuals manifest a tendency to jump to conclusions, and the degree to which they do this may be related to the strength of delusional thinking (e.g. Garety & Freeman, 1999). Studies of attributional style focussing on patients with delusions of persecution have shown that such patients manifest a propensity to blame other people, or external circumstances for particular events (e.g. Bentall et al., 2001). Attention studies suggest that patients with persecutory delusions preferentially attend to threatening stimuli (e.g. Fear et al., 1996).

3.3. Impairments in theory of mind in schizophrenia

In addition to these attentional and reasoning styles, patients with delusions of persecution are behaviourally characterised by a preoccupation with intentions of other people, which may affect the psychological processes involved in forming accurate social beliefs about others (Blackwood et al., 2001). In fact, it has been argued that an impairment in TOM accounts for delusions of persecution. In other words, in these individuals, there is abnormal processing of other people's intentions and mental states in which intentions (usually malevolent) are over-attributed to others (Frith, 1992). Frith proposed that TOM skills develop normally in people with delusions of persecution, but are "lost" during an acute psychotic episode (Frith, 1992). Consequently, persecutory delusions reflect false beliefs about other people's intentions, especially when directed towards the self. Thus it has been suggested that the TOM impairment refers specifically to a problem in computing metarepresentation. This affects the normal decoupling mechanism involved in mentalising, such that schizophrenic patients with delusions of persecution do not detach the content of a representation from the real world. As a result, people's beliefs are misconstrued as aspects of the real world, and this type of TOM impairment results in positive symptoms of schizophrenia, including delusions of persecution and auditory hallucinations (Frith, 1994).

The model proposed by Bentall and colleagues (e.g. Kinderman & Bentall, 1997), integrates attributional style with TOM impairments to explain delusions of persecution. They argue that the characteristic style of avoidance of internal attributions (not accepting responsibility for especially negative events) arises from dysfunctional strategies for regulating self esteem. TOM deficits consequently ensure that intentions and actions are attributed to other people rather than situational factors (Kinderman & Bentall, 1997).

Autism and schizophrenia, while phenomenologically distinct, are both proposed to share the feature of impairment in TOM. However, the models of a mindreading *deficit* that exist to explain autism seem unlikely to account for social cognition problems in schizophrenia. While autism is characterised by a deficit in attributing mental states to others (Baron-Cohen et al., 1985; Frith et al., 1991), the presence of positive symptoms in schizophrenia is more commonly associated with *over*-attribution of mental states,

biases to certain types of mental states and the *over*-attribution of one's personal affectedness in a given social interaction. For example, it has been shown that patients with delusions of persecution interpret others' non-intentional actions as being intentional (Corcoran, 2003) and non-causal actions as being causal (Blakemore et al., 2003a). Thus, people with positive symptoms of schizophrenia are not "mind-blind"; they demonstrate an awareness that other people have intentions and beliefs, but in a qualitatively different way to both autistic and healthy individuals. This has been described as "over-mentalising" (ascribing beliefs and intentions *wrongly*) in schizophrenia, and "under-mentalising" in autism (*failing* to ascribe beliefs and intentions) (Frith, 2004)).

It has thus been argued that these positive symptoms of schizophrenia can be explained in terms of a "disturbed capacity in patients to relate their own intentions to executing behaviour, and to monitor others' intentions" (Frith, 1992; see Brüne, 2005, for a recent review). TOM has been extensively studied in schizophrenia but findings are inconsistent. In spite of the fact that delusions are the most prevalent psychotic symptom associated with schizophrenia (Breier & Berg, 1999), there is little consensus as to the relationship with social cognitive task performance, for example in mentalising tasks. Schizophrenia is a heterogeneous disorder; it is especially unclear as to how different symptom subgroups might show particular impairments. This may be because of the inclusion of patients with several types of symptoms in one patient group that is compared to a healthy control group. In general, understanding one's own and others' mental states has been found to be impaired in schizophrenic populations compared to healthy controls, in support of Frith's (1992) neuropsychological account (Corcoran et al., 1997; Corcoran & Frith, 1996; Langdon & Coltheart, 2001; Mitchley et al., 1998; Sarfati et al., 1997; Sarfati et al., 1999).

Most of the studies tapping TOM in schizophrenia employ verbal or pictorial tasks that require participants to make inference about social meanings. For example, a 'hinting task' was used by Corcoran and colleagues (1995), which involved the interpretation of short stories about social interactions between two characters, and required participants to infer the intentions of characters from indirect speech. The phrase, "It's very cold in here", for example, was expected to be taken to mean, "Please shut the window". Patients with negative symptoms performed worst, even when IQ was co-varied out.

Paranoid patients also demonstrated difficulty compared to controls, while patients with passivity symptoms and those in remission were no worse than controls. This suggested that TOM performance is a state rather than a trait variable. Similarly, in another study by Frith and Corcoran (1996), patients with paranoid symptoms performed worse than patients with passivity symptoms and controls, on first and second order false belief tasks. However, the finding that TOM impairment is specific to persecutory delusions has not been consistent.

The appreciation of humour similarly involves the understanding of the intentions of characters and how events are causally related. While the appreciation of jokes was shown to be impaired in schizophrenia generally (Corcoran et al., 1997), when broken down into patient subgroups, both patients with passivity and paranoid symptoms performed more poorly than controls. Picture sequencing, illustrating series of vignettes, has also been used to test the ability to represent other agents' intentions in schizophrenia (Sarfati et al., 1997; Sarfati et al., 1999) and results indicated that TOM impairments were specific to schizophrenic patients with formal thought disorder.

More recently, the understanding of visual jokes, including 'physical' or 'mental state' jokes, was found to be compromised in schizophrenic patients, compared with healthy controls, matched for age, sex and estimated IQ (Marjoram et al., 2005). Schizophrenic patients were particularly impaired in comprehension of mental state jokes, indicating a specific link between TOM impairment and schizophrenia, in support of previous findings (e.g. Corcoran et al., 1997). Marjoram and colleagues explored the notion that specific positive symptoms are linked to TOM impairments (Corcoran et al., 1995; Frith & Corcoran, 1996) but found no correlation between TOM impairment and positive symptom severity, even when specific symptoms of delusions and hallucinations were scrutinised (Marjoram et al., 2005).

The over-inference of malevolent intentions to other people is thought to be the result of abnormal causal attributions to external agents (Fear et al., 1996; Kinderman & Bentall, 1997). The studies described above have used complex social stimuli involving verbal and pictorial vignettes. The processing of basic components of social information in schizophrenia was investigated in a task that required participants to rate mechanically or intentionally moving shapes on a computer screen according to their level of agency

(Blakemore et al., 2003a). This study found that psychotic patients with delusions of persecution had a higher tendency than psychotic patients without delusions of persecution or healthy control groups to attribute contingency to the intentional stimuli. This was thought to reflect the behavioural tendency of these patients to over-attribute intention and mental states to others, which leads to the conviction that others have malevolent intentions related to patients. However, this study did not test whether abnormal attribution of intentions was more likely when intentions were directed to the self.

In addition, in a study by Corcoran and Frith (2003), in which tasks involved the comprehension of stories about social interactions and false beliefs, schizophrenic patients were impaired on TOM performance and this was related to an impairment in autobiographical memory. This was thought to reflect an alternative analogical reasoning strategy among schizophrenic patients when thinking about others' intentions and beliefs. This finding might also suggest a relationship between impaired *self*-consciousness and consciousness of *others* in schizophrenia. Blackwood and colleagues (2001) relate the role of self-related information to TOM impairments in everyday social interactions, predicting that normal social inferences, which require selection of social data in the environment that is relevant to the self, and then accurate inferential processing to determine others' intentions towards the self, are impaired in schizophrenia. They propose that this type of processing requires information from the "self schema," that is, accurate encoding and integration of information about the self in relation to social contexts. How the understanding of one's own and other people's mental states relate specifically to positive symptoms in schizophrenia remains unexplored.

3.4. Experiment 2: Perspective taking in patients with positive symptoms of schizophrenia

3.4.1. Introduction

This study on perspective taking in schizophrenic patients with positive symptoms probes the question of whether atypical processing of other people's intentions and mental states, as demonstrated by performance on complex TOM tasks as well as basic causality tasks, is also reflected in the ability to take the first-person and third-person

perspective in socio-emotional contexts. Social cognitive skills, such as having a TOM, that is, the ability to infer other people's thoughts, intentions and desires (Baron-Cohen, 1995; Frith & Frith, 2003), and empathy, the vicarious response to affective cues from another person in a specific situation (Hoffman, 1978) are central to successful social interaction, and rely on the ability to represent what others think (Frith & Frith, 2003; Premack & Woodruff, 1978). As described above, their absence or poverty is characteristic of social communicative disorders such as autism and schizophrenia (Frith, 2004).

In order to investigate further the nature of TOM impairments in autism and schizophrenia, Langdon et al. (2006) clarify the distinction between epistemic and non-epistemic mental states. These authors discuss autistic individuals' problems with mentalising tasks involving intentions and beliefs (epistemic) but show that these individuals have no problems with visual perspective taking tasks or in understanding simple emotions (non-epistemic). On the other hand, individuals with schizophrenia do manifest problems in visual perspective taking tasks (Langdon et al., 2001) and show a different quality of impairments in TOM tasks. Langdon and colleagues hypothesise that the problem in autism may be a "domain-specific" problem of de-coupling epistemic mental states from reality, but that in schizophrenia, the problem lies in a "domain general" impoverishment in simulating other people's subjective worlds.

This suggestion is supported by their data from an emotion attribution study (Langdon et al., 2006). This study investigated how patients diagnosed with schizophrenia, relative to healthy controls, performed on a TOM task, an emotion attribution task (similar to an emotional perspective taking task) and on an emotion identification task. The results demonstrated that the patient and control groups were equally able to identify emotional expressions, but the patients had significantly more difficulty with emotion attribution and false belief inference. The authors suggest that, unlike in autism, people with schizophrenia may have a general difficulty in empathic perspective taking that affects their ability to infer other people's beliefs *as well as* their direct appreciation of others' emotions and perceptions. However, while Langdon and colleagues do relate TOM impairment to schizophrenia, this study did not distinguish between different symptom subgroups of schizophrenia, each of which, as described earlier, seems to relate differently to TOM task performance.

The ability to take another's perspective is crucial for successful social communication. In order to reason about others, and understand what they think, feel or believe, it is necessary to step into their 'mental shoes' and take their perspective. As described in the previous chapter, perspective taking includes awareness of one's own subjective mental states ("first-person perspective", or 1PP) and the ability to ascribe mental states to another person ("third-person perspective" or 3PP). Emotional perspective taking is related to first-order TOM in that it involves surmising what another person is thinking or feeling. While perspective taking requires the representation of the mental states of others (epistemic), it does not require entering into an affective state oneself (de Vignemont & Singer, 2006). However, perspective taking also requires the attribution of emotions to oneself and to others. The appreciation of emotional states, itself, is therefore also required to successfully perform this task (non-epistemic).

Here, emotional perspective taking was investigated in a hospitalised group of adult patients with affective disorders and minimal positive symptoms of schizophrenia (P-group) and a second group of patients with strong positive symptoms of schizophrenia (predominantly, delusions of persecution) (P+), compared with healthy, normal controls (NC), using a computerised question-and-answer task that required participants to consider their own response to certain emotional situations or those of another person in the same situations.

As in the previous perspective taking experiment (Chapter 2) involving typically developing adolescents and adults, in this study, the efficiency and strategy of processing of 1PP and 3PP emotional perspectives were contrasted. The measure of interest was the difference in RT between the two perspective conditions, that is 3PP-1PP (Δ RT). Given the evidence for mindreading deficits and the reports of difficulties to "enter into another's feelings" (Lee et al., 2004), it was considered possible that the efficiency and style of perspective taking in the P+ group would differ from the clinical and healthy control groups. Given that the link between TOM and positive symptoms has so far been equivocal, the relationship between symptom severity, as indexed by the positive subscale of the PANSS interview (Kay et al., 1987), and Δ RT was additionally explored.

With respect to emotional valence of TOM impairments in schizophrenia, apart from the notion that *negative* intentions are often attributed to external agents (Frith, 1992), evidence from epidemiological studies, questionnaire and experimental data suggest that there is a link between negative beliefs, often in relation to the self, and the development of symptoms of psychosis (cf. Smith et al., 2006). Several explanations have been put forward including the theory that symptoms of psychosis such as delusions offer a protective element against a background of negative emotions (Bentall et al., 1994) or that negative emotions have a direct causal role in the development of delusions and hallucinations that become involved in the appraisal of negative beliefs and emotions (Garety et al., 2001). Furthermore, anhedonia, the decreased ability to experience pleasure, has been linked to schizophrenia, and is manifest behaviourally through flattened responsivity and emotional bluntness (Meehl, 1962; Rado, 1953). At the cognitive level, it is hypothesised that this association between negative emotion and the positive symptoms of schizophrenia is reflected by a "negative emotion-specific deficit" in emotion identification and discrimination tasks (Johnston et al., 2006). However, results have been inconsistent in this respect and emotion identification studies have generally focused on the valence of emotions related to the self. In the current study, the tendency to select negative, positive and neutral emotional responses relating to the self *and others* was analysed to investigate the hypothesised link between negative and flattened affect and social cognitive processing in schizophrenia. Given the tendency to over-attribute malevolent intentions to other people, it was predicted that there would be a bias in the emotional valence on the responses in the delusional group, compared to the other groups, such that they would have a preference for negative emotions over neutral or positive emotions in the answer choices, particularly when these related to other people.

3.4.2. Method

3.4.2.1. Participants

A group of 25 in-patients (two male) from the Department of Psychiatry at the Centre Hôspitalier de Versailles, and 11 healthy university students (five males) in Paris, France gave consent to participate in this study. All patients were diagnosed by clinical interview using the ICD-10 (International Classification of Diseases; WHO, 1992). Patients included those with diagnoses of affective disorders including depression and bipolar disorder, and those with a diagnosis of schizophrenia. At the time of testing, all

patients were medicated. They were taking anti-depressant, anti-psychotic, hypnotic or anxiolytic medication. All but two patient participants had been in education at least to the level the Baccalaureate (French examination equivalent to A-levels). All control participants had taken the Baccalaureate and were in further education or employment. Written informed consent was obtained from the participants. The study was approved by the local ethics committee. Data from eight of the recruited patients were excluded because these patients did not complete the task.

3.4.2.2. Measure of positive symptoms

All patients were divided into two groups according to the presence or absence of positive symptoms which included delusions and auditory hallucinations. This was determined according to the PANSS interview (Kay et al. 1987), conducted by psychiatrists. The PANSS is a 30-item 7 point (1-7) rating instrument of psychotic symptoms. The interview is divided into three sections: positive subscale, negative subscale and general psychopathological subscale. Here, only positive subscale scores were used. The positive subscale comprises seven questions which rate delusional ideation, conceptual disorganisation, hallucinations, excitation, delusions of grandeur and persecution and hostility. Each question can be scored from 1 (absence) to 7 (extreme). The maximum score for the positive subscale is 49 (see Appendix 3B). The PANSS interview was administered to patient groups only. Those patients whose scores were between 7 and 14 on the positive subscale, indicating the absence of, or minimal, delusions or auditory hallucinations, were classified as not experiencing positive symptoms (P- group). Those who scored 15 or over were classified as experiencing positive symptoms (P+ group). The control group consisted of healthy adults with no previous history of psychiatric or neurological disorders. In the P+ group, all patients were suffering from delusions of persecution, except one who was mainly experiencing auditory hallucinations.

There were thus three participant groups: NC (normal controls; N=11); P- (patients with minimal or no positive symptoms; N=10); P+ (patients with strong positive symptoms; N=7, after exclusions). Categorising the groups in this way, rather than by diagnosis, enabled the investigation into the contribution of positive symptoms *per se* to the processing involved in the perspective taking task. The presence of patients without positive symptoms (P-) ensured that other 'global' factors that might affect performance

(e.g. attention, reaction speed as a result of medication or hospitalisation) were also controlled for. The mean score on the positive symptoms subscale for the P+ group (21.0±3.1) was significantly higher than that of the P- group (12.1±7.1) ($Z=-2.7$; $p<0.01$).

3.4.2.3. Experimental design

Participants were presented with blocks of scenarios, written in French. The questions in this task were modified from those used for the task in Chapter 2, in order to make them suitable for adults instead of children and adolescents, and then translated. First, a one-line sentence describing an everyday scenario was presented on a laptop computer screen together with a question concerning how the participant himself or herself (for 1PP scenarios), or how the protagonist (for 3PP scenarios), would feel in such circumstances (See Figure 3.1). The number of characters and clauses in each scenario were matched between conditions. There were 120 trials altogether, of which half conveyed the question in the first person ("Comment vous sentez-vous?" / "How do you feel?") and the other half asked the same question but about a hypothetical character in the third person ("Comment se sent-il/elle" / "How does he/she feel?"). The participant was instructed to press the space bar after reading the question at his or her own pace. This elicited the presentation of two possible response choices in the form of simple cartoon faces, each representing one of five possible emotions: very happy, happy, neutral, sad, afraid and angry. The participant was asked to choose, as quickly as possible, one of the two faces in answer to each question. As soon as the participant responded, the next scenario appeared. Reaction times (RT), taken as the time in milliseconds (ms) between the presentation of the answer screen and the key press for the chosen answer, were recorded by the computer. The actual task was preceded by a Practice session in which participants were trained to ensure correct emotion attribution to each face. See Methods, Chapter 2.

Perspective. Scenarios either concerned 1PP or 3PP – see Chapter 2 and Appendix 3A.
Choice type. Answer choices were either Open or Closed. See Chapter 2.
The design and rationale for the factors above were exactly as described in the Methods section of Chapter 2, which also contains details of the Experimental Procedure and Instructions which were replicated from the first experiment, but in French.

3.4.2.4. Data analysis

3.4.2.4.1. Reaction time differences between all three groups

Non-parametric tests were used for this analysis because the data were not normally distributed. For each participant, median RTs were calculated for each of the four conditions of 1PPO, 1PPC, 3PPO and 3PPC. The difference between the median RT for 1PP and 3PP was then calculated for each participant (Δ RT). Overall Δ RT, as well as Δ RT for each of the Open (Δ RT-O) and Closed (Δ RT-C) conditions were compared between the three participant groups (NC, P- and P+) using a Kruskall-Wallis test. Post-hoc Mann-Whitney U tests, corrected for multiple comparisons, were used to investigate further between-group differences.

3.4.2.4.2. Individual differences between patients

Given that the presence of positive symptoms existed on a continuum, beyond a specific diagnosis of schizophrenia, the results of all patients were also analysed together in one group to test the hypothesis that the severity of positive symptoms (range of score: 7 – 31) predicted performances on the different conditions of the perspective taking task. A Spearman's rank correlation investigated the relationship between the score on the positive subscale and Δ RT in each of the Open and Closed conditions. Here, Spearman's rank correlation was used in view of the relatively low N.

3.4.2.4.3. Emotional valence of response

Each question was followed by a choice of two cartoon faces depicting emotions. Altogether, six emotions were presented: very happy, happy, neutral, sad, afraid and angry, i.e. two positive, one neutral and three negative. An equal number of positive and negative expressions were used in the task. The neutral faces were only appropriate to the Open condition, and were therefore used less than the positive and negative faces. For each participant, the total number of positive, neutral and negative response choices in each condition (Positive-Open, Positive-Closed, Negative-Open, Negative-Closed, Neutral-Open) were calculated and converted to percentages.

An average percentage was calculated for each group and a Kruskall-Wallis test was used to compare the relative percentages of the valence of each emotion response between groups. Any main effects were further explored using Mann-Whitney U tests to

analyse specific between-group differences and to investigate any differences between the Perspective conditions.

3.4.2.4.4. Error analysis

Response choices in the Closed condition were subject to an error analysis. The percentage of errors were calculated for the 1PPC and 3PPC conditions for each subject, and a Kruskall-Wallis test was used to compare the percentage of errors between groups. The Open condition, by definition, was not amenable to such an error analysis, given that both response choices for each question are designed to be equally valid.

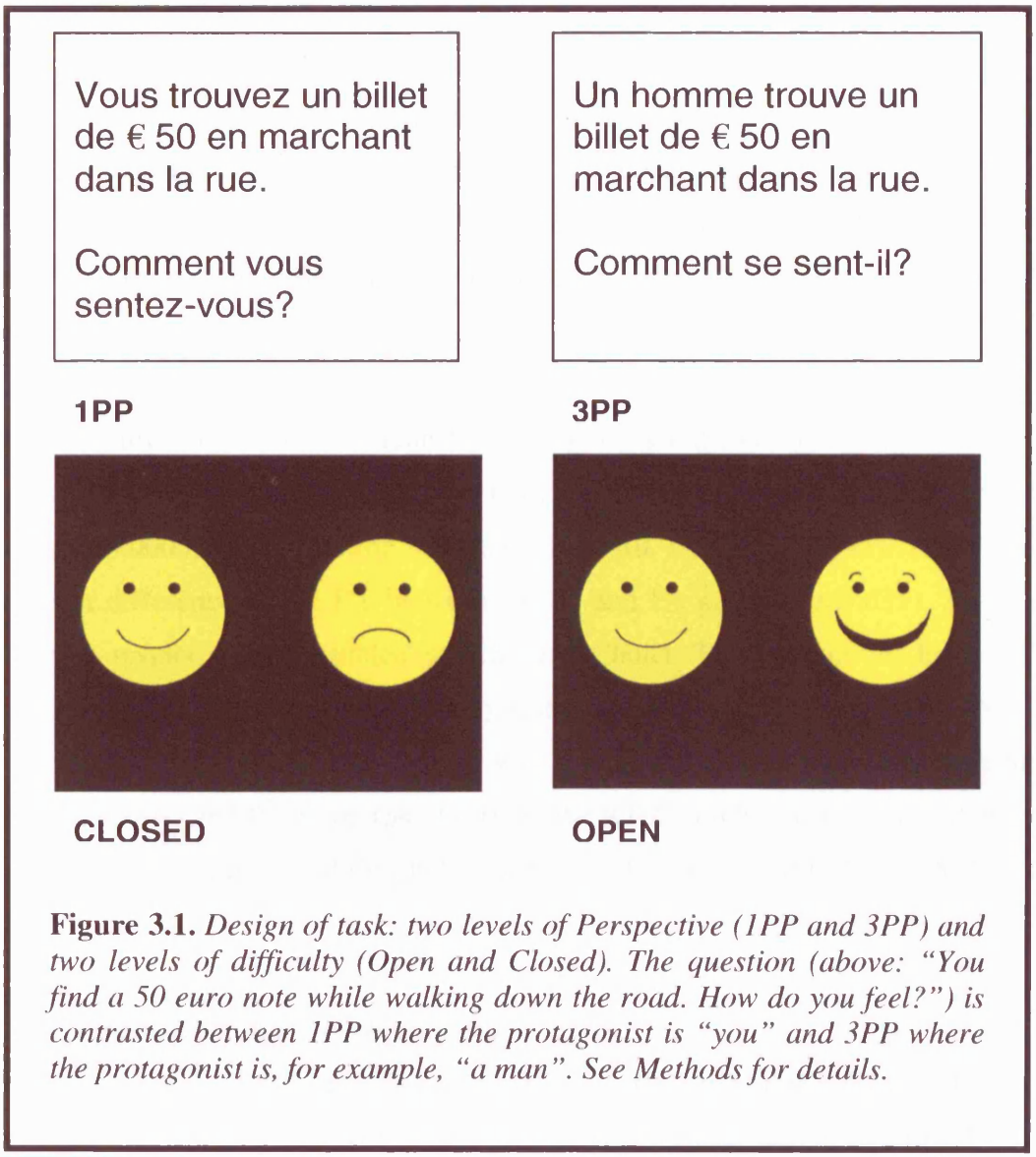

Figure 3.1. *Design of task: two levels of Perspective (1PP and 3PP) and two levels of difficulty (Open and Closed). The question (above: "You find a 50 euro note while walking down the road. How do you feel?") is contrasted between 1PP where the protagonist is "you" and 3PP where the protagonist is, for example, "a man". See Methods for details.*

3.4.3. Results

One further patient was excluded from the P+ group and one participant was excluded from the NC group on the basis of the RT data being outliers (overall RT was over 3 S.D. away from the mean in the group). The remaining participants were able to follow the instructions and complete the task.

3.4.3.1. Overall reaction time comparison between groups

A Kruskall Wallis test showed that there were main effects of Group (NC/P-/P+) on overall RT (χ^2=17.1, d.f.=2, p<0.0001). This effect was the same for RT in each Choice Type condition (main effect in RT-O condition: χ^2=16.7, d.f.=2, p<0.0001; RT-C condition, χ^2=17.4, d.f.=2, p<0.0001).

Post-hoc Bonferroni-corrected Mann-Whitney U-tests indicated that the overall RT to answer questions was significantly lower in the NC group than in the P- group (N_{NC}=10, N_{P-}=10, p<0.0005) as well as the P+ group (N_{NC}=10, N_{P+}=6, p<0.005). There was no significant difference in the RT between the P- and P+ groups (p=0.635). See Figure 3.2. These results were paralleled within each Choice Type condition. In the RT-O condition, the NC group was significantly faster than both the P- group (p<0.0001) and the P+ group (p<0.001). The NC group was also significantly faster than both the P- group (p<0.0001) and P+ group (p<0.0001) in the RT-C condition. However, there were no differences in either condition between P- and P+ groups (RT-O: p=0.562; RT-C: p=0.713).

3.4.3.2. Differences in Δ RT between groups

Δ RT was used as the measure of proficiency in perspective taking. It is the difference between the RT for 3PP and 1PP (Δ RT = 3PP-1PP). These differences in RT (Δ RT) were absolute differences, not taking into account direction of difference between 3PP and 1PP. There was a main effect of Δ RT in the Closed condition (Δ RT-C) (χ^2=7.8, d.f.=2, p<0.05) (see Figure 3.4). There was additionally a near-significant main effect of Δ RT in the Open condition (Δ RT-O) (χ^2=5.98, d.f.=2, p=0.052) (see Figure 3.3). There was no significant effect of Group on the overall Δ RT (χ^2=4.9, d.f.=2, p<0.085, *n.s.*).

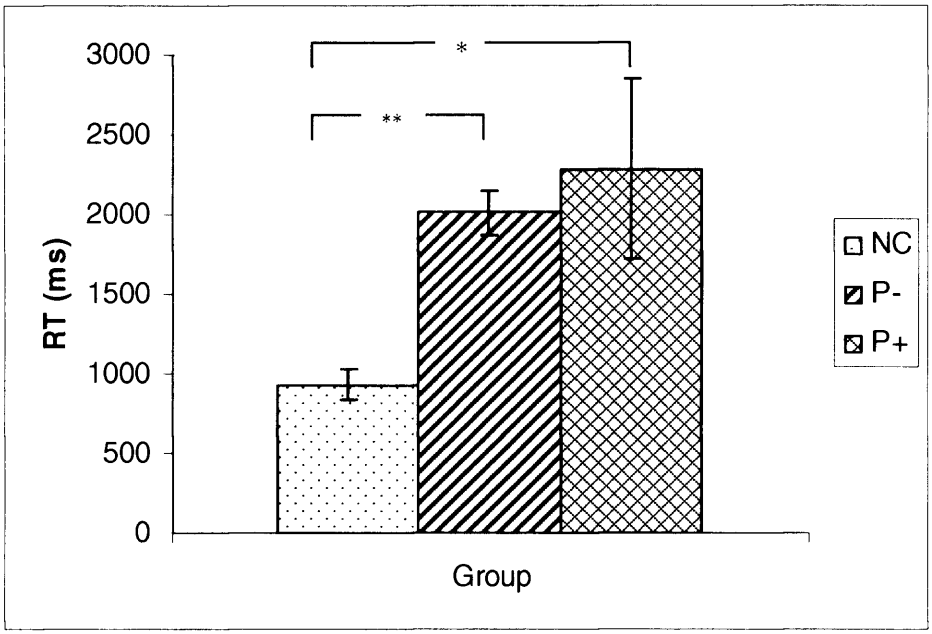

Figure 3.2. *Overall RT differences between groups. NC group (N=10) answered questions significantly faster than both the P- group (N=10) and the P+ group (N=6). There was no RT difference between the P- and P+ groups.*

[=p<0.005; **=p<0.0005]*

Post-hoc Bonferroni corrected Mann-Whitney U-tests demonstrated that, while there was no difference in Δ RT-O between groups (for NC vs. P-, p=.070; NC vs. P+, p=.112; P- vs P+, p=.792) (see Figure 3.3), Δ RT-C was significantly higher in the P- compared with NC group (p<.005). However, there were no differences in Δ RT-C between the NC and P+ groups (p=.713) or between the P- and P+ groups (p=.44) (See Figure 3.4).

3.4.3.3. Investigating directionality of Δ RT

In order to explore the variance and strategy or 'style' of responses within groups, individual data points were plotted showing Δ RT in both directions of 3PP>1PP and 1PP>3PP for each participant group.

The variance in Δ RT showed little difference between groups in the Open condition, although on looking at the graph there was slightly less variance in the NC group compared to the patient groups (see Figure 3.5). On the other hand, the graph shows that in the Closed condition, the variance, as well as the pattern of directionality of Δ RT was different between groups (see Figure 3.6). The Δ RT-C graph shows that the variance in the NC group was lower than that among the P- and P+ groups. Furthermore, while the NC participants showed a relatively low Δ RT with most participants, while clustering close to the zero-line (3PP=1PP), taking marginally longer in the direction of 3PP>1PP, in the P- group, 36% of participants had a Δ RT in this direction of 3PP>1PP, while 64% of P- participants had a Δ RT in the direction of 1PP>3PP. However, perhaps in view of the low N, this difference in directionality between groups was not statistically significant (χ^2=0.343, d.f.=2, p=0.842).

This pattern was exaggerated in the P+ group such that all bar one had a Δ RT in the direction of 1PP>3PP. In comparison, in the Δ RT-O condition (Figure 3.5), the distribution of Δ RT was relatively even in either direction of 1PP>3PP and 3PP>1PP for all groups.

3.4.3.4. Effect of positive symptoms on Δ RT

To explore individual differences between patient participants, the P- and P+ were collapsed and Δ RT in each condition was correlated with the PANSS positive subscale score for all patients. Spearman's rank correlations showed no significant relationship

between PANSS score and Δ RT-C (rho=-0.27, p=0.315, *n.s.*) or Δ RT-O (rho=0.33, p=0.22, *n.s.*).

In summary, there was a near-significant main effect of Group on Δ RT-O, but post-hoc tests showed no significant differences between groups. There was a significant main effect of Group on Δ RT-C that arose from the P- group having a significantly higher Δ RT-C than the NC group. Directionality of Δ RT-C was explored to investigate this further. Although between group tests were non-significant, perhaps due to a low N, in the Δ RT-C (in which there was a main effect of Group), the P+ group showed a particular Δ RT-C bias in the direction of 1PP>3PP.

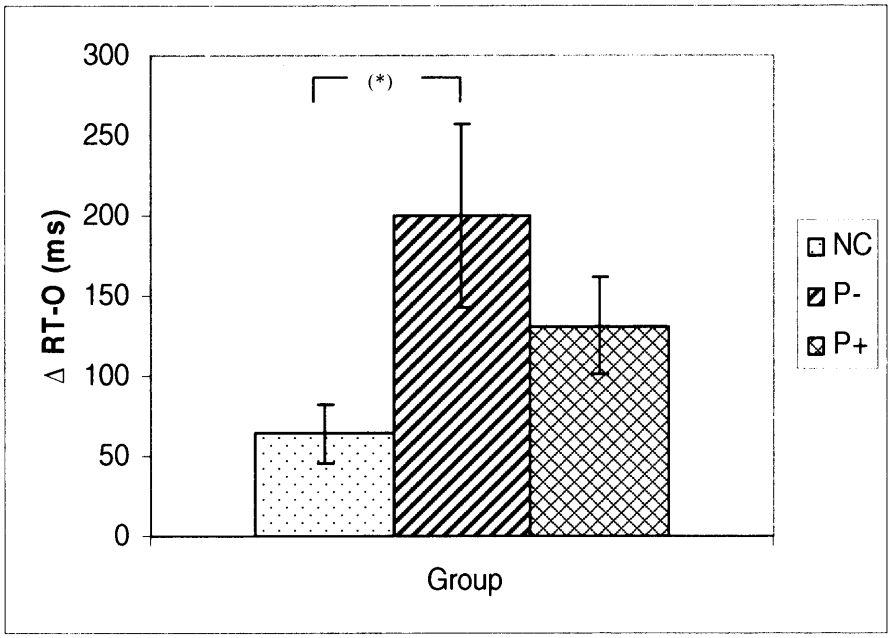

Figure 3.3. *Δ RT-O for each group. There was a near significant main effect of Group on Δ RT-O but post-hoc tests between groups showed no significant differences. [(*) = trend of p=0.07]*

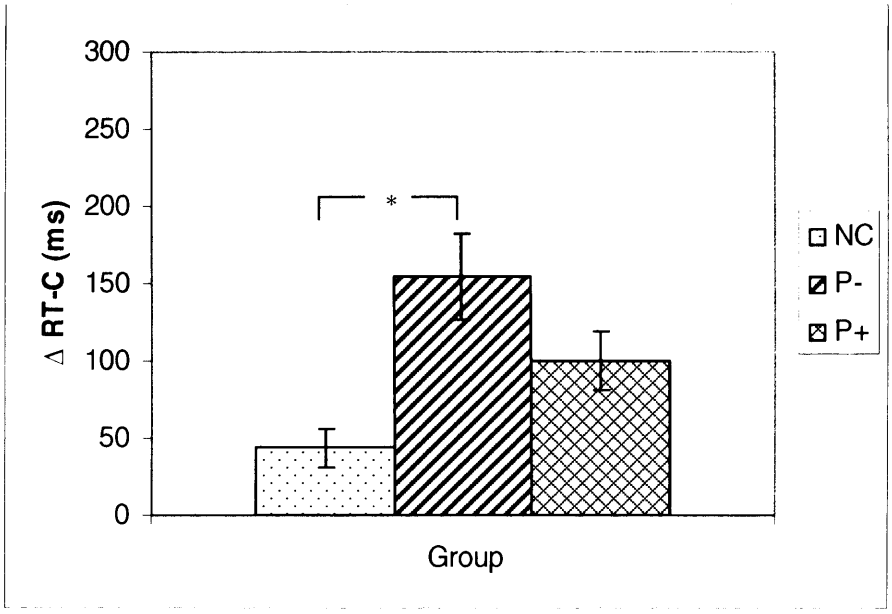

Figure 3.4. *Δ RT-C for each group. There was a significant main effect of Group on Δ RT-C. Post-hoc tests indicated that Δ RT-C was significantly greater for the P- than the NC group. There was no RT difference between the P- and P+ groups or between NC and P+ groups. [*=p<0.005]*

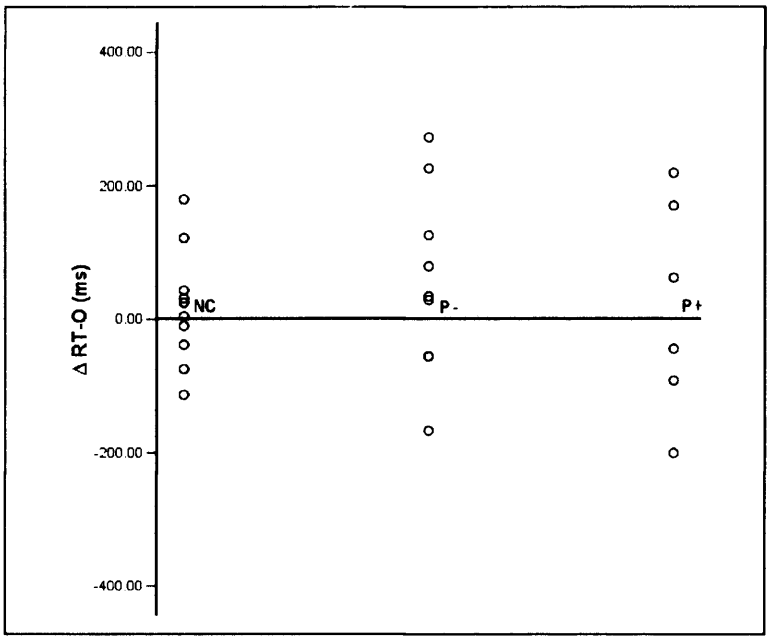

Figure 3.5. ***Variance and directionality of Δ RT-O in each group.*** *As can be seen in the graph, there was little difference in variance between groups. Δ RTs are spread approximately evenly in both directions of 1PP>3PP (below x-axis) and 3PP>1PP (above x-axis) for all groups.*

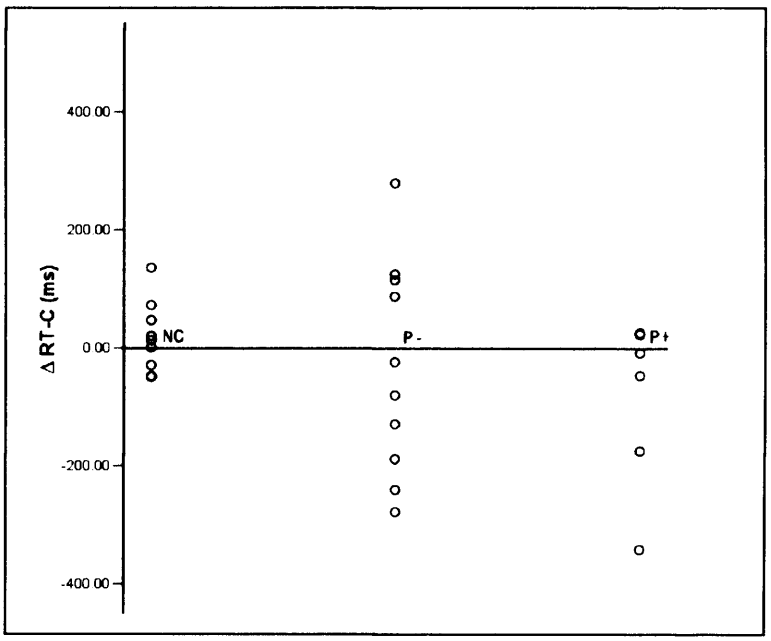

Figure 3.6. ***Variance and directionality of Δ RT-C in each group.*** *The graph suggests that variance was lower in the NC group compared to the P- and P+ groups. The direction of Δ RT shifted from predominantly 3PP>1PP in the NC group to relatively higher in the 1PP>3PP direction in the P- group to almost all in the 1PP>3PP direction in the P+ group.*

3.4.3.5. Difference in emotion choices between groups

A Kruskall-Wallis test, comparing the percentage of responses selected in each emotion category between groups, indicated a main effect for both the positive (POS-C; $p<0.05$) and negative (NEG-C, $p<0.05$) emotion categories in the Closed condition, and for the neutral condition (NEUT-O, $p<0.005$). Post-hoc Mann-Whitney U tests, Bonferroni-corrected for multiple comparisons, indicated that the main effect of NEUT-O arose from the significantly higher percentage of NEUT responses in the P+ group (mean % ±S.E.=10.4±2.0%) compared to the NC group (4.6±1.2%) ($p<0.05$), and the significantly higher percentage of NEUT responses in the P- (9.2±1.2%) group compared to the NC group ($p<0.05$). The difference in the percentage of NEUT responses was not significant between the P- and P+ groups. In addition, the percentage of POS-C responses in the P+ group (46.7±1.5%) was significantly lower than that of the NC group (51.4±0.7%, $p<0.05$). The percentage of NEG-C responses in the P+ group (53.3±1.5%) was significantly higher than that of the NC group (48.6±0.7%, $p<0.05$). See Figure 3.7.

The significant effects of POS-C, NEG-C and NEUT-O were further analysed for effects of self (1PP) and other (3PP), using Bonferroni-corrected Mann-Whitney U tests. No differences between groups were found in the percentage of POS-C and NEG-C responses depending on whether the emotions related to the self or other. However, the significant difference in percentage of neutral responses chosen between groups arose from between-group differences in the 3PP. The percentage of neutral responses in the 3PP condition was significantly lower in the NC (mean % ± S.E.=2.8±0.69%) than in the P- group (7.8± 2.2%) ($p<0.01$), and similarly, significantly lower in the NC compared with the P+ (9.3±2.2%) group ($p<0.05$). There was no difference between P- and P+ groups in the tendency to select neutral responses in the 3PP condition ($p=0.713$). See Figure 3.8.

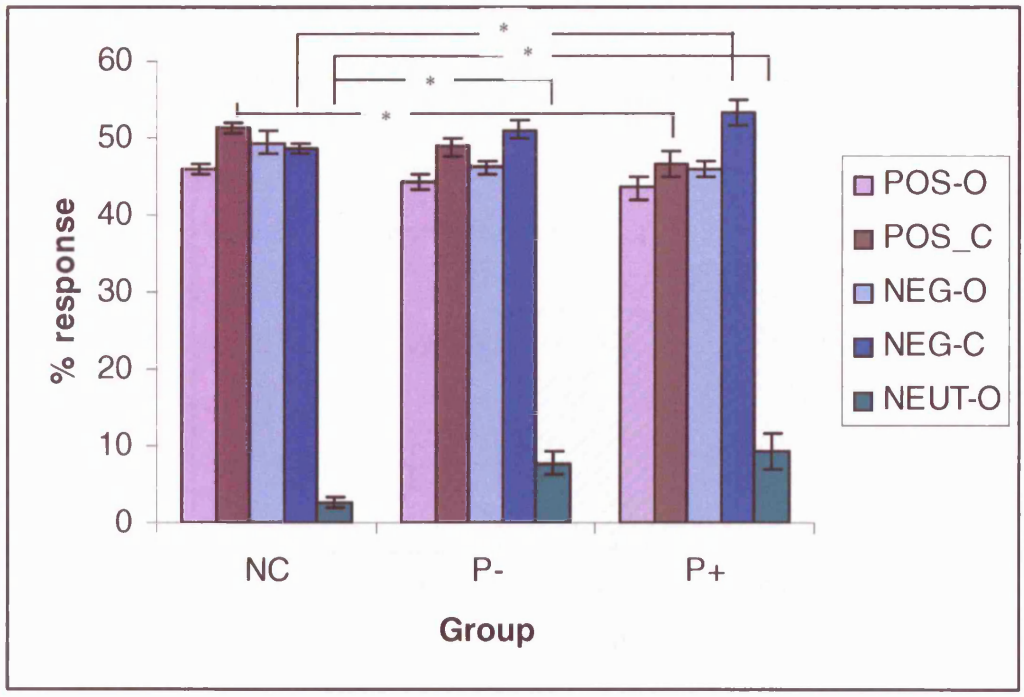

Figure. 3.7. *Percentage (%) of responses in each emotion category for each group. There was a main effect of POS-C, NEG-C and NEUT-O.*

[=p<0.05]*

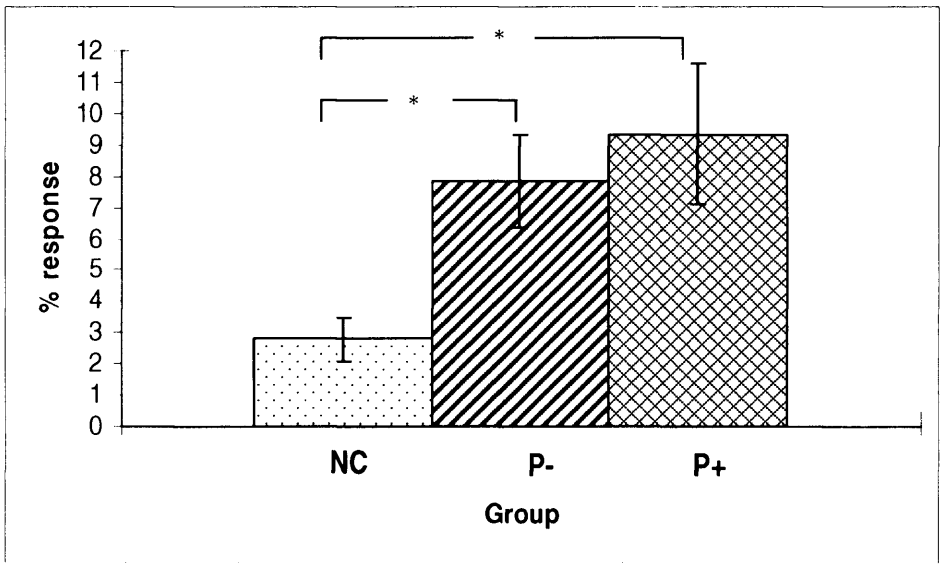

Figure 3.8. *Comparison of % neutral responses in the 3PP between groups. P- and P+ groups selected significantly more neutral responses in the 3PP than the NC group. There was no difference in % neutral responses between the P- and P+ groups.*

In summary, the NC group chose more positive (and fewer negative) responses than did the P+ group in the Closed condition. In the Open condition, compared with controls both patient groups chose a higher proportion of neutral responses when answering questions about someone else (3PP).

3.4.3.6. Error analysis

There were no differences in the percentage of errors made in the Closed condition between groups (χ^2=1.3, d.f.=2, p=.518, *n.s.*). This analysis cannot be performed for the Open condition because there are no errors in this condition, by design. In the Open condition, either of the two answers offered is equally appropriate.

3.4.4. Discussion

To investigate the hypothesis that people with schizophrenia have an impairment in the ability to mentalise, this study used a modified version of the task described in Chapter 2 tailored to adults and translated into French, tapping perspective taking in patients with schizophrenia and those with affective disorders. Patients were classified by the degree of positive symptoms experienced, which were predominantly delusions of persecution but included hallucinations (minimal positive symptoms: P-; high level of positive symptoms: P+). The difference in RT between 3PP and 1PP (Δ RT) was compared between groups, in each Choice Type (Open/Closed) condition (Δ RT-C and Δ RT-O). As in the previous chapter, Δ RT was used as a measure of proficiency at perspective taking. In light of the previously hypothesised reduction in the ability to experience pleasure in schizophrenic and depressed patients and a bias towards experiencing negative beliefs and emotions in schizophrenic patients, the tendency to respond with each of the emotional valences of the responses was compared between groups.

The results demonstrated a main effect of group in the Δ RT-C but not the Δ RT-O condition. The main effect in the Δ RT-C condition was due to the significantly higher Δ RT among P- patients compared to NC participants. Directionality of Δ RT in the Closed condition suggested a pattern, albeit non-significant, of Δ RT bias in the direction of 1PP>3PP in the P+ group. Analysis of emotion choices indicated that P+ patients selected a significantly higher percentage of negative, and lower percentage of

positive, responses compared to NCs. In addition, the percentage of neutral responses in the 3PP was significantly higher in the P- and P+ groups compared to NCs.

3.4.4.1. Differences in general task efficiency between groups

There was a significant effect of Group (NC/P-/P+) on overall RT taken to perform the task in both the Open and Closed conditions. Both P- and P+ groups were significantly slower than the NC group, but there was no difference in speed between the two patient groups. This RT difference most likely reflects the difference in motor speed, concentration and motivation between control and patient participants. Indeed, considerable motivational differences to perform the task were also noted between patients and controls, at the time of testing. In addition, the lack of RT difference between P- and P+ groups suggests that medication may have had an impairing effect on reaction speed. Both patient groups were medicated at the time of testing. Antipsychotic and antidepressant drugs are well-known to have a slowing effect on psychomotor speed, as well as an impairing effect on memory. Time taken in between the question and response screen to recall the previous scenario, coupled with a slower motoric response and reduced motivation may account for this general RT effect.

3.4.4.2. A mentalising impairment in patients with affective disorders?

As described in the previous chapter, Δ RT was used as an index of proficiency on the perspective taking task. While a comparison between groups in Δ RT-C demonstrated a significant effect, there was only a trend in Δ RT-O. Post-hoc tests indicated that in the Closed condition, NC participants had a significantly lower Δ RT than P- participants. No significant differences were found between the NC and P+ groups, or between the P- and P+ groups. Why should the absolute (non-directional) difference in RT between 3PP and 1PP be higher in the patients with affective disorders who were experiencing low levels or no positive symptoms of schizophrenia, compared to healthy controls? A higher Δ RT-C in the P- group might suggest that this group of depressive and bipolar patients is particularly impaired at perspective taking. The pronounced difference in RT between 3PP and 1PP suggests that relative to NCs, P- patients show self and other perspectives that are maximally separated in terms of processing time. If, as suggested by NC adults here and in Chapter 2, the lack of difference in RT between 3PP and 1PP is indicative of fast and instinctive (automatic) perspective taking, then this result for the P- group suggests these patients are particularly inefficient in making the

translocations between self and other. This is in line with previous data to suggest that people with affective disorders are impaired in their ability to mentalise (Inoue et al., 2004; Kerr et al., 2003; Lee et al., 2004).

3.4.4.3. Different strategies for perspective taking between NC, P- and P+ groups?

What do these data say about perspective taking in the P+ group, however? Given the low N, further information about the form of processing might be gleaned from looking at the directionality of Δ RT. Absolute (non-directional) RT differences, in other words, might mask differences in strategy. As Frith (2004) points out, results of performance in schizophrenic patients with delusions on TOM tasks are equivocal, perhaps because it is difficult to elucidate the exact strategy, or style, of mentalising that leads to poor performance. Interpretations about differences in patient and control strategies may be extrapolated from the graph (Figure 3.6) demonstrating the distribution of Δ RT-C in both the 1PP>3PP and 3PP>1PP directions. Given the significant main effect of Group for Δ RT-C, the directionality for this condition was further investigated to understand qualitative differences in the strategy of response. This graph suggests a difference, albeit statistically non-significant, in the strategy of perspective taking between groups, which is masked by comparing only absolute, non-directional RT differences. With larger groups, these differences may have been statistically significant.

The previous data set on the development of perspective taking in Chapter 2 demonstrated that normal adults have a minimal difference in RT between 3PP and 1PP and that the mean Δ RT is around 50ms with a range of approximately 100ms in either direction. The current data corroborate this previous finding, showing that NC adults have a relatively small Δ RT, clustering tightly within a similar range to the adults in the previous normative study of perspective taking in this thesis. In the current study, as Figure 3.6 demonstrates, the Δ RT of NC participants are clustered close to the zero-line, although spread marginally in either direction, with the majority showing a minimally higher RT for 3PP relative to 1PP. The variance between participants is considerably greater for the P- group, and participants in this group have significantly higher Δ RT, with most taking longer to answer 1PP questions compared with 3PP. Between the NC and P- group, therefore, there is a shift from approximately equal efficiency for self- and other-related questions, to a tendency to take longer for scenarios involving the self compared to those involving other people.

In the previous chapter, it was argued that in adults, social experience and mature brain circuitry associated with perspective taking account for equal efficiency for taking the 1PP and 3PP. In a forced choice situation, when choosing between two answers designed to be unambiguous, perhaps affective patients tend to deliberate for longer on how they imagine themselves emotionally responding to each scenario. This may be because they can generate and/or access first-person simulations elicited by the 1PP questions, whereas they are impaired in the ability to generate third-person simulations in response to the 3PP questions, and therefore answer 3PP questions using a fast rule-based strategy ("what people would generally feel"). This is consistent with the notion that people with affective disorders are impaired in their ability to decode other people's mental states (Inoue et al., 2004; Kerr et al., 2003; Lee et al., 2005), as measured by, for example, performance on a task involving inference of mental states from photographs of eyes (Lee et al., 2005).

The scatterplots (Figures 3.5 and 3.6) suggest that variance between P+ patients was not dissimilar to that between P- patients. However, the scatterplot for Δ RT-C (the condition for which there was a main effect of Group) indicates that in the P+ group, the pattern of directionality found in the P- group was more exaggerated such that the direction of Δ RT among P+ patients was heavily biased in the direction of 1PP>3PP. In other words, there was a tendency of schizophrenic patients with strong positive symptoms to take longer in responding to questions relating to how they themselves, felt, compared to those questions relating to how other people feel. A possible interpretation could be that a longer RT for 1PP is indicative of participants engaging more in the 1PP. This effect, perhaps due to the low N of six, was not, however, statistically significant. The pattern may, though, suggest a particular impairment in taking the perspectives of other people in the P+ group. This is in line with findings from studies of schizophrenic patients showing poor performance relative to controls on TOM tasks. For example, schizophrenic patients exhibiting delusions of persecution or thought disorganisation score less highly than healthy controls on a variety of social cognition tasks, that employ picture-sequencing (Brunet et al., 2003; Sarfati et al., 1997; 1999), cartoon stories (Frith & Corcoran 1996; Pickup & Frith 2001) jokes (Corcoran et al. 1997) and irony (Mitchley et al. 1998). Increased variance in the patient groups compared with the control group may be suggestive of a less consistent and less systematic processing strategy for perspective taking.

3.4.4.4. An impairment in self-consciousness in schizophrenia?

On the other hand, as suggested in the Introduction, a tendency to take a longer time to answer questions in the 1PP might alternatively reflect difficulty in answering these questions, relative to the 3PP questions. Looking at Figure 3.6, the graph would suggest, then, that P- and P+ patients are able to take the 3PP given the relative efficiency for 3PP compared with 1PP in most cases, particularly in the case of P+ patients (Figure 3.6). This is consistent with results of a previous study of meta-representation in delusional schizophrenics (Gambini et al., 2004). This study showed that some delusional patients gain insight about their mental state when the perspective is shifted from the first- to the third-person perspective. In other words, they were impaired in thinking about their own mental state from their own perspectives. Perhaps the tendency for patient groups to take a longer time to answer questions in the 1PP compared to the 3PP, especially among those experiencing a higher level of positive symptoms of schizophrenia, reflects impairment in self-consciousness.

Conscious reflection relating to the self might therefore be anomalous in schizophrenia (Frith, 2004). Self-monitoring and self-consciousness in the context of motor control is proposed to be anomalous in schizophrenia, although this evidence is from patients with delusions *of control* (Blakemore et al., 2000), hallucinations and formal thought disorder (Kircher & Leube, 2003). People diagnosed with schizophrenia who have delusions of control often report that their movements, thoughts and emotions feel as if they are under the control of some other agent rather than caused by their own volition. Self-produced action is assigned to an external agent, rather than to the self, such that the movement feels involuntary. Studies of such patients have led several groups to interpret the cause of this experience as a failure in the self-monitoring system (Frith, 1987; Frith et al., 2000; Johns et al., 2001). Indeed, patients with delusions of control or auditory hallucinations have different experiences of self-tickling, compared with healthy controls or other patient controls who do not exhibit the symptoms (Blakemore et al., 2000). There appears to be a failure in attenuation in the self-touch condition, such that the self-touch feels as intense and tickly as external touch. This suggests that something may have gone awry in the predictive mechanism that usually serves to reduce the sensory consequences of self-generated actions. A breakdown in the forward model might, therefore, account for the feeling that active movements are passive and the attribution of such sensations to alien sources.

One speculative interpretation about the underlying mechanism of perspective taking in the P+ group in the current study is that this fault in self-monitoring might extend to the higher social cognitive domain in patients with delusions of persecution (Blakemore & Decety, 2001). Indeed, it has been argued that patients with passivity symptoms can perform normally on TOM tasks because their representation of others' mental states is preserved, while their representation of their own mental states is impaired (Pickup & Frith, 2001). If this can be extended to patients with delusions of persecution, this interpretation would argue that thinking about one's own mental states, therefore, is harder in affective patients compared with healthy controls, and particularly impaired in schizophrenic patients. Both interpretations – about an impairment in self-consciousness (1PP) or other-consciousness (3PP) – are compatible with neuroimaging studies that indicate atypical functioning of inferior PFC in schizophrenic patients during a source-monitoring task (Spence et al., 1997), of inferior frontal gyrus during a mentalising task (Russell et al., 2000) and of PFC during an intention attribution task (Brunet et al., 2000). This parietal brain area is related to agency and self-consiousness (e.g. Lou et al., 2004) and the frontal areas are related to TOM (e.g. Gallagher and Frith, 2003).

No relationship was found between symptom severity, as measured by the positive subscale of the PANSS interview, and Δ RT, contrary to the prediction. However, the patients here included those with both delusions of persecution and auditory hallucinations. It is possible that different symptom types have different influences on social cognitive processing. One study showed that patients with auditory hallucinations tended to make greater misattributions of agency (Johns et al., 2001). However, in the study by Marjoram et al. (2005) described earlier, TOM impairments showed no relationship with positive symptom severity in patients with delusions of persecution. A larger sample of patients, broken down into symptom subgroups would be helpful to further investigate the proposed link between symptom severity and perspective taking.

It is possible that that the graph for Δ RT-O (Figure 3.5) does not suggests obvious differences in strategy between groups because the Open condition is more difficult, by design, and therefore engages more 'thoughtful' responses rather than what might be the default pattern shown in the Closed condition.

3.4.4.5. No impairment in epistemic mental state representations in schizophrenia?

A third alternative, given the lack of statistical difference between NC and P+ groups in either absolute Δ RT or directional Δ RT, is that there is no difference between these groups in the ability to represent other people's mental states, as gauged by this particular perspective taking task. It is possible that this task is not sensitive enough to detect it. Or, it is possible that schizophrenic patients with delusions of persecution do not have a specific problem in the decoupling mechanism involved in mentalising. This would suggests that they are in fact able to understand the relationship between the content of a representation and the real world and generate the correct mental state representations of other people and make the necessary distinctions between the self and other states ("epistemic" representations (Langdon et al., 2006), that is the ability to infer how someone would feel based on the knowledge of that person and/or their behaviour or context). Langdon and colleagues (2006) have suggested that there is a domain general problem in TOM in schizophrenia, such that these patients have an impairment in representing emotional states in others (that is, in "non-epistemic" representations, that involve direct appreciation of emotional meaning). However, the task also involves representing basic emotions in the first place. Thinking about how other people feel, in this context, thus involves both non-epistemic states as well. The following section discusses how the current data do suggest a difference between healthy controls and P+ patients in emotional understanding and attribution, which may reflect differences between P+ and NC individuals in non-epistemic representation.

3.4.4.6. A bias towards more negative and less positive emotion choices in schizophrenia

Several studies have investigated emotion recognition in schizophrenia and have reported atypical performance relative to normal controls (e.g. Hermann et al., 2006; Kee et al., 2006; Lee et al., 2006; Phillips et al., 2003). Atypical emotion processing has been consistently found in schizophrenia across different cultural groups, including North American, German, Indian and South African Xhosa patients (Habel et al., 2000; Leppänen et al., 2006). The nature of the differences from control groups has, however, been shown to be inconsistent among all patients. Mirroring the notion that schizophrenic patients demonstrate a negative bias and an enhanced experience of negative emotions compared to normal controls (Barrowclough et al., 2003; Meehl, 1962), the current data show that there was a main effect of Group on the percentage of

positive responses and negative responses chosen in the Closed condition such that the NC group chose significantly more positive and significantly less negative responses than the P+ group in the Closed condition.

This difference between the NC and P+ groups is consistent with some studies that have shown that schizophrenic patients experience positive emotions such as joy and interest less frequently than normal (e.g. Suslow et al., 2003), that they also have an automatic attentional bias towards negative threatening stimuli (e.g. Green & Phillips, 2004) and that they have a specific deficit in processing a subset of negative emotions such as anger, fear and sadness recognition (Bediou et al., 2005; Silver et al., 2002). These studies have focused on the experience of attributing or recognising emotions relating to the self. Results from other studies, show no specific emotion deficit, even relating to the self, in schizophrenic patients (e.g. Johnston et al., 2006; Kee et al., 2006). These inconsistent results may arise from the differences in patient subgroups according to symptoms as well as emotion stimuli. Some studies have shown atypical emotion processing when emotional stimuli are modulated to make them more arousing for example, high intensity angry faces (e.g. Leppänen et al., 2006). In the current task, emotions were basic and did not differ in their degree of intensity. However, this would be an interesting line of modification to the task in future research.

3.4.4.7. Misinterpreting neutrality in other people in affective and schizophrenic patients

The analysis of the emotional valence of the responses also demonstrated a main effect of Group on the percentage of neutral responses chosen. Neutral faces, which appeared only in the Open condition, were chosen significantly more frequently by the P- compared to the NC group, and also by the P+ compared to the NC group. There were, however, no significant differences in the tendency to select neutral responses between the two patient groups.

The significant effects of emotional valence (in the POS-C, NEG-C and NEUT-O) were further analysed to investigate any differences between 1PP and 3PP. No differences between perspective conditions (1PP vs. 3PP) were found for the positive or negative emotions, in support of one study which did analyse attribution of negative beliefs to others, but found that was no particular tendency of the group of delusional

patients studied to attribute negative evaluations to other people (Smith et al., 2006). A difference in percentage response between 1PP and 3PP was found only in the neutral condition, such that the P+ group selected a significantly higher percentage of neutral responses in the 3PP compared to the NC group. Similarly, there was a significantly higher percentage of neutral responses selected by the P- group compared to the NC group. This propensity of patients to select more neutral responses may explain why the Δ RT pattern was found to be different in the Open and Closed condition. In the Open condition, the variance was similar in all three groups and the distribution of Δ RT was spread more evenly in both directions, compared to the Closed condition, in which there was a bias in patients towards the 1PP>3PP direction, which was most pronounced for P+ group.

Previous findings have suggested that schizophrenic patients are prone to misinterpreting intended meanings of subtle or ambiguous emotional cues (cf. Kee et al., 2006). For example, in emotion identification tasks, they tend to have higher error rates in neutral expression identification, misattribute other emotions to neutral faces, for example falsely attributing anger to neutral expressions (Kohler et al., 2003; Leppänen et al., 2006) or seeing ambiguity as threatening (Phillips et al., 2003). A recent ERP study investigating decoding of emotional expressions demonstrated higher error rates in the neutral condition and curiously, higher ERP amplitudes over parietal areas during the neutral condition in schizophrenic patients (Hermann et al., 2006). This was taken to reflect increased brain activation during neutral faces, possibly linked to a tendency of schizophrenic patients to look actively for information in neutral situations. This effect was pronounced in paranoid compared to non-paranoid patients, in parallel with behavioural reports linked to paranoid schizophrenic patients misinterpreting neutrality as affect in other people. The tendency of the P+ compared to the NC group to attribute more neutral faces to others (that is, in the 3PP) might be associated with a specific proneness to making errors and looking for emotional cues in the neutral condition, that would in turn lead to increased RT in the 3PP relative to 1PP. Similarly, depressed patients have been shown to bias the recognition of emotionally neutral faces (e.g. Leppänen et al., 2004). In this study, depressed patients took especially long and were less accurate relative to healthy controls in recognising neutral faces, compared to other basic emotional expressions.

The error analysis in this task was limited to the Closed condition here, in which there was one clear correct and one clearly incorrect answer. The analysis showed no significant difference in errors in patients compared to controls. In the Open condition, either of the answers can be correct (e.g. happy vs. neutral / sad vs. afraid), and was therefore not amenable to error analysis. That the increased tendency to select neutral responses in the P+ group reflects an increase in erroneous responses is therefore speculative, but it was noted at the time of testing that emotion identification was considerably more unstable in the patients groups compared to the control group. Even though the task was preceded with a training session to ensure that participants were correctly assigning emotions to faces, several of the patients in both the P- and P+ groups exhibited an inability to correctly identify facial expressions, asking questions about the faces during the task.

3.4.5. Conclusion

Mentalising impairments have previously been reported in patients with schizophrenia, but findings about the nature of these problems, especially in relation to particular symptoms, have been inconsistent. Perspective taking, related to first order TOM, was investigated in patients with schizophrenia and affective disorders, with varying degrees of positive symptoms, particularly delusions of persecution. Comparisons in the difference in RT between 3PP and 1PP (Δ RT) between patients with higher (P+) and lower (P-) levels of positive symptoms and normal controls (NC) indicated that P- patients had a significantly higher Δ RT than the NC group in the Closed condition. An exploration of strategy suggested a bias among patients, particularly in the P+ group, such that they took longer to answer questions in the 1PP compared to the 3PP, perhaps suggesting an impairment in self-consciousness. Analysis of emotion choices indicated that P+ patients chose fewer positive and more negative responses compared to NCs. Both P- and P+ groups chose more neutral responses when they related to other people (3PP) than did NCs perhaps because these patients are impaired in decoding ambiguous expressions in other people.

The next study investigates how the understanding of the relationship between one's own intentions and the consequent actions develops during adolescence.

THINKING ABOUT ONE'S OWN INTENTIONS

CHAPTER 4

4. DEVELOPMENT OF INTENTION UNDERSTANDING DURING ADOLESCENCE

4.1. What is intention understanding?

Intentional understanding refers to the ability to look at the actions of an object or agent and predict what it is going to do, and that its actions and/or mental states can be *about something* (Dennett, 1987). Dennett described how we can understand the actions of entities from different stances. One approach would be to take a physical stance, which would involve applying the principles of physical sciences to an object in order to link its actions with the consequences. On the other hand, taking an intentional stance would mean assuming that the entity has a mind and therefore goals, desires or beliefs, which are most likely to influence its behaviour (see Introduction, Chapter 1). Actions and their consequences would thus be linked by the mental states of the agent. The intentional stance is therefore suited to understanding the behaviour of agents. In the following study, the development of the neural circuitry underlying the ability to predict the actions that result from self-related intentions during adolescence was investigated.

Given the socialisation process associated with the adolescent period, in which interactions with others play an important role, it might be expected that components of mentalising, such as the ability to understand how intentions govern actions, are refined with age. Evidence for the development of brain areas associated with mentalising suggests that neural maturation may support this cognitive development.

4.2. Experiment 3: Development of intention understanding during adolescence

4.2.1. Introduction

As explained in Chapter 1, it has recently been demonstrated that the brain undergoes development during the period of adolescence, particularly in areas of the brain that are linked to TOM. These brain areas include PFC and STS. Histological studies coupled with MRI data suggest that changes in grey and white matter are accounted for by the process of synaptic pruning and myelination, respectively (see Toga et al., 2006). It is thought that the functional consequences of synaptic pruning and myelination are increased efficiency and fine-tuning of neural networks (see Blakemore & Choudhury,

2006a).

Based on the finding that PFC and STS undergo structural development during adolescence, it was hypothesised that the functioning within these regions would also show developmental change during this time period. Many high-level cognitive abilities rely on these brain regions, including mentalising (or Theory of Mind; Frith & Frith, 2006). Mentalising refers to the inferences that we naturally make about other people's intentions, beliefs and desires, which we then use to predict their behaviour. It includes the understanding that intentions relate to actions. A number of neuroimaging studies, using a wide range of tasks, have reported activation in a highly circumscribed "mentalising network," comprising the MPFC, the STS and temporo-parietal junction (TPJ), and the temporal poles adjacent to the amygdala (Brunet et al. 2000; Castelli et al. 2000; Fletcher et al. 1995; Gallagher et al. 2000; Vogeley et al. 2001). Lesion studies have also implicated the frontal cortex in mentalising (Channon & Crawford, 2000; Gregory et al. 2002; Happé et al., 2001; Rowe et al., 2001; Stone et al., 1998; Stuss et al., 2001; though see Bird et al., 2004) and STS/TPJ (Apperly et al., 2005; Samson et al., 2004).

Signs of social competence develop during early infancy, such that by around 12 months of age, infants can ascribe agency to a system or entity (Johnson, 2003; Spelke et al., 1995). The understanding of intention emerges at around 18 months, when infants acquire joint attention skills, for example, follow an adult's gaze towards a goal (Carpenter et al., 1998). These early social abilities precede more explicit mentalising, such as false belief understanding, which usually emerges by about five years of age (Barresi & Moore, 1996; Leslie, 1994; Rochat et al., 2004; Schlottmann et al., 2002). While normally developing children begin to pass TOM tasks by about age five, the brain structures that underlie mentalising undergo substantial development beyond early childhood. It was hypothesised that the functioning of brain areas involved in mentalising tasks may change during adolescence. Functional imaging of the adolescent brain provides an opportunity to investigate this development.

To this end, a mixed factorial design was employed, with the factors i. *Causality* (intentional causality vs. physical causality) and ii. *Age group* (adults vs. adolescents). In the Intentional Causality condition, the subject's task was to answer blocks of

questions posing scenarios that involved their own intentions and consequential actions. The Physical Causality condition involved answering questions about the causal link between physical events and their consequences. In a previous study looking at adults only, the Intentional Causality task, relative to the Physical Causality task, was found to activate regions associated with mentalising (MPFC, STS and temporal poles) and self-reflection (MPFC and posterior cingulate/precuneus) (den Ouden et al., 2005).

The objective of this study was to investigate whether the adult brain and the adolescent brain process this intentional causality task differently. While some functional neuroimaging studies have shown that activation of frontal cortex increases with age (e.g. Adleman et al., 2002; Kwon et al., 2002; Rubia et al., 2000), others have demonstrated the reverse pattern (e.g. Casey et al., 1997; Gaillard et al., 2000; see Blakemore & Choudhury, 2006b and Introduction, Chapter 1, for details).

4.2.2. Method

4.2.2.1. Participants

19 right-handed, female adolescents (mean age: 14.79; age range: 12.12 - 18.06 years) and 11 right-handed female adults (mean age: 28.43; age range 22.40 - 37.76 years) with no history of psychiatric or neurological disorder took part in the study. To ensure a consistent level of verbal intelligence across all participants, the British Picture Vocabulary Scale (BPVS; Dunn et al., 1997) was administered individually to each participant. Furthermore, adult subjects were university students or graduates, and the adolescent subjects were from a selective private school in London at which the vast majority (about 95%) of pupils go on to do undergraduate degrees and higher. The school teachers confirmed that each adolescent subject performed above average on national SAT tests. Written informed consent was obtained from all participants, and from the parents of the participants aged 16 and under, prior to the study, which was approved by the National Hospital for Neurology and Neurosurgery Ethics Committee.

4.2.2.2. Experimental design

The experiment was split into two 11 minute sessions. Subjects were presented with a description of a scenario followed by a question relating to this scenario. Each block consisted of three scenario/question trials. In half the blocks, scenarios pertained to intentions and consequential actions (*intentional causality (IC)*): e.g. *scenario stimulus*:

"You are at the cinema and have trouble seeing the screen"; followed by *question stimulus*: "Do you move to another seat? Likely or Unlikely?." In the other blocks, the scenarios pertained to natural occurrences and consequential events (*physical causality (PC)): e.g. scenario stimulus*: "A huge tree suddenly comes crashing down in a forest"; followed by *question stimulus*: "Does it make a loud noise? Likely or Unlikely?". In each block, the scenario stimulus was presented for 4.7 seconds, and was immediately followed by the question stimulus. The question stimulus was presented for 4.7 seconds, during which time subjects were asked to respond by pressing one of two buttons on a keypad corresponding to "likely" and "unlikely". The scenarios and questions were matched between the two conditions in terms of number of characters, words and clauses (see Appendix 4).

In addition to the two conditions described above (IC and PC), a baseline condition was included in which subjects were asked to fixate on a black cross on a white background for a duration of 30 seconds. There were eight repetitions of each of the three conditions. Block order was counterbalanced within and between subjects. Each subject was trained on the task for approximately 4 minutes prior to scanning. Stimulus presentation was programmed in Cogent (www.vislab.ucl.ac.uk/Cogent/index.html) running in Matlab 6.5, which recorded subject responses.

4.2.2.3. Data acquisition

A 1.5 T Siemens Sonata MRI scanner was used to acquire both 3-D T_1-weighted fast-field echo structural images and multi-slice T_2^*-weighted echo-planar volumes with blood oxygenation level dependent (BOLD) contrast (TR = 3.6secs). For each subject, functional data were acquired in two scanning sessions of approximately 11 mins each in which 195 volumes were acquired. The first 5 volumes were discarded to allow for T1 equilibrium effects. Each functional brain volume was composed of 40 2mm axial slices with a 1 mm gap, and in-plane resolution of 3x3x2 mm positioned to cover the whole brain. The acquisition of a T1-weighted anatomical image occurred after the two sessions for each participant. The total duration of the experiment was approximately 35 minutes per subject.

4.2.2.4. Data analysis

4.2.2.4.1. Behavioural data analysis

Mean reaction times and response types were calculated for both IC and PC questions. The main effects of causality (IC vs. PC) and age, as well as the interaction between causality and age, were analysed using a mixed design ANOVA.

4.2.2.4.2. Functional neuroimaging analysis

For data analysis statistical parametric mapping was used, implemented in SPM2 [http://www.fil.ion.ucl.ac.uk/spm]. For each subject, a set of 380 fMRI scans was realigned to correct for interscan movement and stereotactically normalised using sinc interpolation (Friston et al., 1995), with a resolution of 3x3x3 mm^3, into the standard space defined by the Montreal Neurological Institute (MNI) template. The scans were then smoothed with a Gaussian kernel of 6 mm full-width half maximum to account for residual inter-subject differences.

The analysis of the functional imaging data entailed the creation of statistical parametric maps representing a statistical assessment of hypothesised condition-specific effects (Friston et al., 1994). The scans corresponding to the instruction phase of each block were excluded from the analysis. Condition-specific effects were estimated with the General Linear Model with a delayed boxcar wave-form for each condition. Low-frequency sine and cosine waves modelled and removed subject-specific low-frequency drifts in signal, and global changes in activity were removed by proportional scaling. Each component of the model served as a regressor in a multiple regression analysis. The resulting parameter estimates for each regressor at each voxel were then entered into a second level analysis where 'subject' served as a random effect in a within-subjects ANOVA. The main effects and interactions between conditions were then specified by appropriately weighted linear contrasts and determined using the t-statistic on a voxel-by-voxel basis.

Statistical analysis at the second level was performed for each group separately to examine the main effect of the two experimental conditions compared with the baseline stimulus, and the main effect of intentional causality [(IC) - (PC)]. Since there were no predictions about differential activation in PC, no PC-IC contrasts were computed. To compare the two age groups directly, the interaction between group (adult vs.

adolescent) and intentional causality task was investigated using the contrasts [(adultIC-adultPC) - (adolescentIC-adolescentPC)] and [(adolescentIC-adolescentPC) - (adultIC-adultPC)]. In addition, the effect of age on each contrast was investigated using a regression function at the second level with age in months as the covariate of interest.

Statistical contrasts were used to create an SPM{t}, which was transformed into an SPM{Z} and thresholded at $p<0.05$ (corrected on the basis of the theory of random Gaussian fields for multiple comparisons across the whole brain volume examined). Regions that survive whole brain correction are reported (or, where there was an *a priori* hypothesis for their activation, small volume correction) at $p<0.05$.

4.2.3. Results

4.2.3.1. Behavioural results

Every subject made a response to every causality question. A mixed design ANOVA revealed that subjects from both groups were significantly faster to answer IC questions than PC questions ($F(1,28) = 89.29$, $p<0.0001$; Figure 4.1). There was no overall significant difference in RT between the two groups ($F(1,28) = 1.92$; $p>0.05$), nor was there a significant interaction between group and task ($F(1,28) = 0.52$; $p>0.05$). There was no significant correlation between age and RTs for either task ($p>0.05$).

4.2.3.2. Functional imaging results

Experimental conditions compared with baseline

Comparison of the two visual conditions with the fixation condition [(IC+PC) - baseline] in both groups resulted in significant activations in regions involved in visual, motor and language processing ($p<0.05$ whole brain corrected), as would be expected.

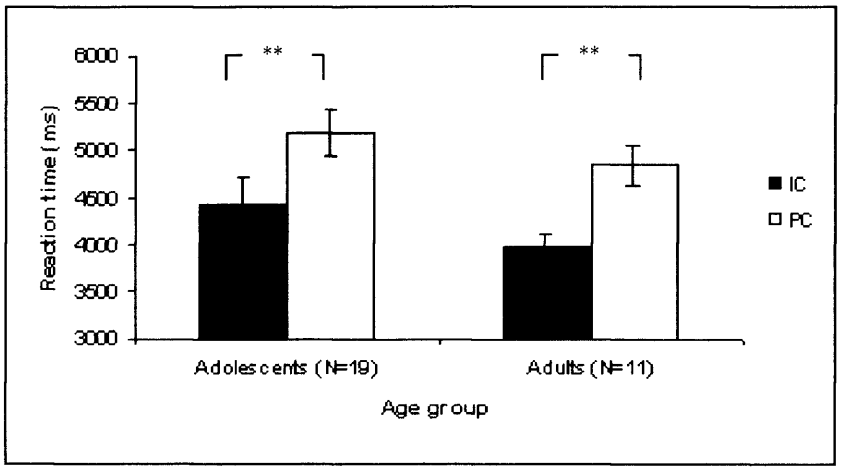

Figure 4.1. *Mean (±S.D.) RTs (ms) in the two conditions for adult and adolescent groups: IC = intentional causality, PC = physical causality. Participants from both groups were significantly faster to answer IC questions than PC questions (F (1,28) = 89.29, p<0.0001. **p=<0.0001*

Main effect of Intentional Causality in both groups

Both groups showed a very similar pattern of activation when comparing questions related to IC scenarios versus questions related to PC scenarios (see Figure 4.2). In both groups, this contrast resulted in activation of the precuneus/PCC, MPFC, temporal poles, STS and TPJ. These activations are listed in Table 4-1 and shown in Figure 4.2.

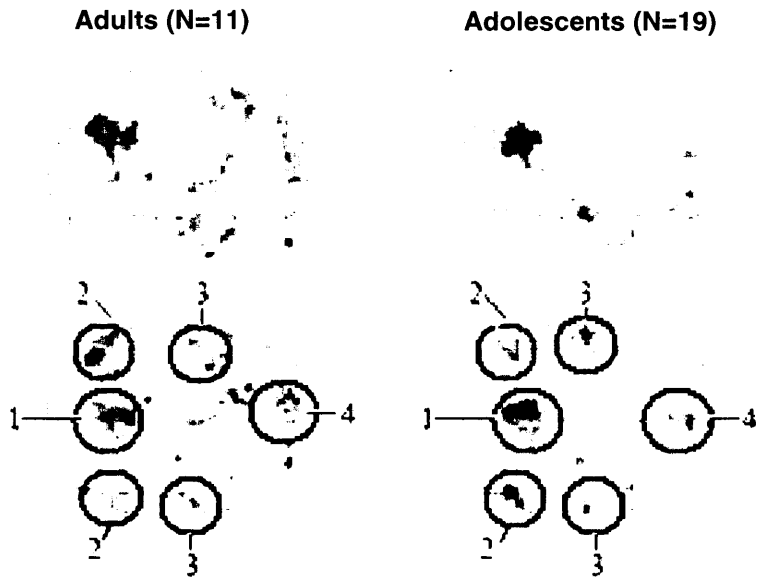

Figure 4.2. ***Main effect of IC-PC in both groups.***

Left panel: *Activation from the adult group (N=11) showing greater activation in the MPFC, precuneus/posterior cingulate cortex, STS, TPJ and temporal pole in the intentional causality (IC) condition versus the physical causality (PC) condition. Anatomical labels: 1. Precuneus/posterior cingulate cortex; 2. STS/TPJ; 3. Temporal pole; 4. MPFC*

Right panel: *Activation from the adolescent group (N=19) from the same contrast (IC-PC). It can be seen that the network of activation in IC-PC is similar in both groups (anatomical labels as in adults' activations)*

Foci of activation	MNI coordinates x	y	z	Z value	Cluster size
ADULTS: Main effect of IC>PC					
Precuneus/posterior cingulate	0	-48	33	4.56	360
L STS	-57	-57	18	3.85	10
L TPJ/intraparietal sulcus	-42	-72	36	4.35	214
R STS	51	-48	24	3.59	47
R TPJ/intraparietal sulcus	48	-75	36	3.54	14
Medial PFC	-9	63	12	3.32	71
L temporal pole	-42	18	-39	3.41	59
R temporal pole	39	21	-33	3.48	24
ADOLESCENTS: Main effect of IC>PC					
Precuneus/posterior cingulate	-6	-51	33	5.51	289
L STS	-45	-60	24	4.22	57
L TPJ/intraparietal sulcus	-45	-72	36	3.64	part of same cluster
R STS	48	-63	21	5.33	60
Medial PFC	0	54	21	4.11	14
L temporal pole	-57	-12	-24	4.75	87
	-45	9	-42	3.54	4
R temporal pole	48	18	-36	4.05	8

Table 4-1. *Coordinates and Z-values for regions of significantly (corrected for multiple comparisons, or SVC) higher activation in the main effect of IC compared with PC.*

Interaction between age and intentional causality

The right MPFC (MNI coordinates: 12 42 21) was activated significantly more in adults compared with adolescents during IC compared to PC ($Z=3.52$; $p<0.05$ SVC) (Figure 4.3 left panel). The regression analysis showed that activity in this region was positively correlated with age ($R^2=0.17$; $p<0.05$; Figure 4.3 right panel).

Conversely, adolescents activated the STS more than did adults when thinking about IC compared to PC (63 –33 –9; $Z=3.35$; $p<0.05$ SVC) (Figure 4.4 left panel). The regression analysis showed that activity in this region was negatively correlated with age ($R^2=0.22$; $p<0.01$; Figure 4.4 right panel).

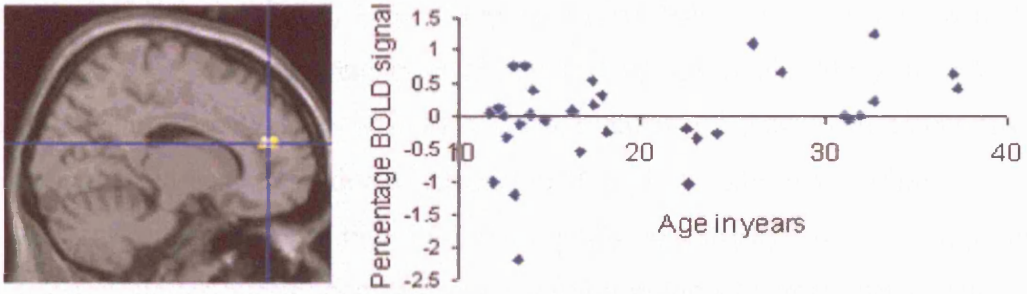

Figure 4.3. *Interaction between group (adults vs. adolescents) and condition (IC vs. PC)* ***Left panel:*** *Activation from the interaction between group and condition, showing greater activity in MPFC in IC-PC for the adult group (MNI: 12 42 21; BA 10) compared with the adolescent group.* ***Right panel:*** *Significant positive regression of BOLD signal in MPFC in IC-PC against age (R^2=0.17; p<0.05).*

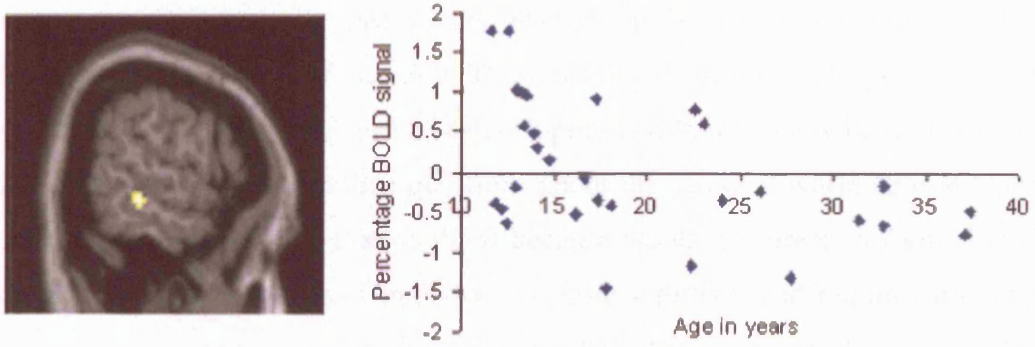

Figure 4.4. *Interaction between group (adolescents vs. adults) and condition (IC vs. PC).* ***Left panel:*** *Activation from the interaction between group and condition, showing greater activity in the right STS in IC-PC for the adolescent group (63 –33 –9) compared with the adult group.* ***Right panel:*** *Significant negative regression of BOLD signal in STS in IC-PC against age (R^2=0.22; p<0.01).*

4.2.4. Discussion

The aim of the present study was to investigate adolescent development of the neural network involved in thinking about intentions. Previous studies have suggested a role for a network of areas (MPFC, STS, TPJ and temporal poles) in this type of mentalising task (Brunet et al., 2000; Gallagher et al., 2000; Vogeley et al., 2001). In the current study, subjects responded to scenarios related either to their own intentions and consequential actions (intentional causality; IC) or to physical events and their consequences (physical causality; PC). This study investigated how activity during these tasks in the adult brain compares with activity in the adolescent brain. The results suggest that activity shifts from posterior to anterior regions of the mentalising network during from adolescence into adulthood.

Both groups of subjects took significantly less time to respond to the IC questions than to the PC questions (Figure 4.1). The difference in reaction times could not have been due to any difference in the structural features of the stimuli since these were matched. Instead, this effect may be due to an inherent difference in cognitive processing demands for the two types of question. These results are in line with previous findings demonstrating a tendency for normally developing children to show better performance on questions about intentions than questions about the physical world (Baron-Cohen et al., 1986). One possibility is that, perhaps because we have "direct" information about intentions, the understanding of intentions is more intuitive, and requires less explicit reasoning and 'working out' than does the understanding of physical causality. This in turn may relate to our ability to simulate intentional causality scenarios relating to people, but not physical causality scenarios relating to objects. There were no significant task performance differences between the two groups.

4.2.4.1. Brain activations associated with intentional causality in both groups

In both adults and adolescents, responding to questions that involved thinking about one's own intentions and consequential actions activated the MPFC, the STS, and the temporal poles (Figure 4.2). These regions are all part of the highly circumscribed neural network that has consistently been activated by mentalising tasks in functional neuroimaging studies across a wide variety of tasks, ranging from attribution of mental states to animated shapes (Castelli et al., 2000; 2002) to understanding beliefs and intentions in cartoons (Brunet et al., 2000; Gallagher et al., 2000; Vogeley et al., 2001)

and in stories (Fletcher et al., 1995; Gallagher et al., 2000; Saxe & Kanwisher, 2003). These areas are proposed to play different roles in mentalising (see Frith & Frith, 2003 for discussion of the functional division between these regions). Activations in the precuneus/PCC in the intentional causality condition relative to the physical causality condition were also found. This region is often activated in tasks that involve thinking about mental states in relation to the self (Happé, 2003; Johnson et al., 2002; Kampe et al., 2003; Kjaer et al., 2002; Lou et al., 2004; Vogeley et al., 2001). The scenarios and questions in the current task related to the self. Therefore, activity in the precuneus/PCC during the IC condition may have been associated with subjects thinking about themselves in the given scenarios.

4.2.4.2. Differences between adults and adolescents

Our results revealed that the MPFC was activated more by adults than by adolescents when thinking about IC relative to PC (Figure 4.3). Activity in this region during IC relative to PC was positively correlated with age. Conversely, the STS was activated more by adolescents than by adults during IC, and activity in this region in this contrast was negatively correlated with age (Figure 4.4). Both these regions are part of the mentalising network. These results suggest that the part of the network that is used to think about intentions shifts from posterior (STS) to anterior (PFC) regions with age over the period of adolescence.

While there were age-related changes in activity in the MPFC and the STS, there was no significant difference between adolescents and adults in activity in the temporal poles (the third region of the mentalising network). Perhaps this is because, unlike the rest of the temporal cortex, the temporal poles mature early, at around the same time as the occipital poles (Toga et al., 2006).

The STS has been proposed to play a role in the prediction of observed patterns of behaviour in order to surmise the mental states underlying this behaviour (Frith & Frith, 2003; Frith, *in press*). This region is activated during the perception of biological motion (Allison et al., 2000; Bonda et al., 1996; Grèzes et al., 2001; Grossman et al., 2000; Puce & Perrett, 2003), of faces and body parts (Campbell et al., 2001; Chao et al., 1999; Grèzes et al., 1998; Puce et al., 1998) and of someone moving their eyes (e.g.

Pelphrey et al., 2005). One possibility is that this region is involved in predicting the trajectory of movements, and higher activity occurs when there is a mismatch between the predicted and actual observed movement (Frith, in press).

The MPFC, in contrast to the STS, is activated whenever subjects reflect on the mental states of themselves or of others (Gallagher et al, 2000; Mitchell et al., 2005; McCabe et al., 2001; Vogeley et al., 2001). In these studies, mental states must often be decoupled from reality; the way we perceive the world is not the way the world is, but the way we believe the world to be. In order to understand another person's mental states, we must be able to decouple what the other person believes about the world from reality - these may be in agreement, but are not necessarily so. Other tasks that activate MPFC involve attributing traits or feelings to people (Mitchell et al., 2002; Schmitz et al., 2004), animals (Mitchell et al., 2005), and oneself (Kelley et al., 2002; Ochsner et al., 2004; Johnson et al., 2002; Lou et al., 2004). All of these tasks involve thinking about mental states. Activity in MPFC is often observed during rest conditions in comparison with high demand tasks (including mentalising). It has been suggested that, during 'rest' or low demand tasks, participants might indulge in spontaneous mentalising (Amodio et al., 2006).

The MPFC has direct connections to the STS (Bachevalier et al., 1997). Frith and Frith propose that the MPFC receives input about the content of mental states and their relation to people's actions from the STS. Consequently the MPFC may be the basis of the decoupling mechanism that distinguishes mental state representations from physical state representations (Frith & Frith, 2003).

4.2.4.3. Development of a strategy for intention understanding

While children start to pass explicit TOM tasks by about five years, our data suggest that the neural basis of TOM continues to develop well past early childhood. Our results indicate a shift with age in recruitment within the mentalising network in the brain, from relatively higher posterior (STS) activation to relatively higher frontal (MPFC) activation from early adolescence to adulthood. Thus, it seems that during adolescence, the neural strategy for thinking about intentional causality changes with age. One possible explanation is that cortical development, including synaptic reorganisation in MPFC and STS (Gogtay et al., 2004; Toga et al., 2006) and increased myelination of

fronto-temporal pathways (Paus et al., 1999), facilitates a change from using more basic social information processing, involving the prediction of another person's behaviour based on their past actions, to more sophisticated mental state inferences in order to predict what action would follow an intention, taking into account future mental states and emotions. Young adolescents might activate mental imagery to predict actions in the IC scenarios, thus eliciting higher activation of the posterior STS. Therefore, young adolescents might use strategies akin to precursors of mentalising to think about intentional causality.

Processing of intentions in adulthood might take a different form. Cortical sculpting during adolescence in frontal and temporal regions might enable a process whereby adults' judgements of what action would follow an intention might be driven by full-blown mentalising. Rather than thinking about the actions *per se*, adults perhaps base their judgements on a representation of the mental states elicited by each scenario, activating the MPFC relatively more highly. In other words, the recruitment of differential neural networks might indicate that adolescents use an action based representation ("What would I do?", based on a prediction of an action) for thinking about intentional causality, whereas adults use mental state representations ("What would I do, given how I would feel?" based on one's own imagined mental states). Adults might additionally be more inclined than adolescents to take into account the mental states of others when making decisions about what action they would take given a particular intention ("What would I do, given how they would feel?" based on the imagined mental states of others). This fits with the proposal that adolescents may be poor at counterfactuals (thinking about "what would happen if...") and therefore tend to be risk taking (Baird & Fugelsang, 2004).

In summary, the STS seems to be concerned with predicting someone else's behaviour on the basis of the past actions, while MPFC is concerned with predicting someone else's behaviour on the basis of future mental states and emotions (e.g. anticipated regret). It is thus proposed that, during adolescence, brain activity shifts from a focus on prediction based on past actions (STS) to prediction based on future mental states (MPFC).

All the questions in this paradigm elicit first-person processing, that is, thinking about what one would do based on one's own intentions. It is not possible to delineate whether increased MPFC activation with age reflects a development in social cognition related to the self *per se*, or mentalising in general. A future extension of this study might include a third-person contrast in the intentional scenarios that elicit processing what one thinks *someone else* would do given their intentions. However, the development of intention understanding in the brain, as suggested by these data, may imply a combination of social cognitive processes related to both self and other. Indeed, as mentioned above, it is proposed that there is a 'default state' of cortical processing involving high metabolic activity at rest in dorsal MPFC, thought to reflect self-referential thinking, which might be expected when task demands are low and participant are free to think about what they like (Gusnard & Raichle, 2001). This suggests that brain activity during self-oriented thinking may overlap with the processing involved in thinking about others (Vogeley et al., 2001). In addition, fMRI studies have demonstrated that reflecting on one's own thoughts or thinking about personality trait adjectives that involve the self elicit activity in similar brain areas to those associated with attribution of mental states to others (Happé, 2003; Johnson et al., 2002, Kelley et al., 2002; Kampe et al., 2003; Kjaer et al., 2002; Lou et al., 2004; Macrae et al., 2004). Self and other might therefore be conceptualized as 'two sides of the same coin', and this 'co-constitution of self and other' (Iacoboni, 2006) suggests that the development found in this study reflects a combination of both self- and other-processing, especially in the context of simulation theory.

4.2.5. Conclusion

Here, the aim was to investigate how the neural system associated with intention understanding changes from early adolescence through to adulthood. The results of this fMRI study revealed that, when thinking about intentional causality (relative to physical causality), activity shifts from posterior to anterior regions of the mentalising network as a function of age. This suggests that the neural strategy for thinking about intentions continues to develop during adolescence and early adulthood. To our knowledge, this is the first imaging study to provide evidence that the mentalising network continues to develop after early childhood. While normally developing children pass TOM tasks by about age five, these data suggest that the mentalising network continues to become refined during adolescence.

The next chapter investigates whether these developments in higher social cognitive skills may be linked to development in the action representation system during adolescence.

THE REPRESENTATION OF ACTIONS IN THE BRAIN

CHAPTER 5

5. THE DEVELOPMENT OF ACTION REPRESENTATION IN ADOLESCENCE

5.1. What is an action representation?

During adolescence, the body is subject to height, weight, organ and musculoskeletal development (Coleman & Hendry, 1990). Internal models might therefore be expected to change with age. An internal forward model, or action representation, is a neural system that simulates the dynamic behaviour of the body in relation to the environment (Wolpert et al., 1995). An internal model can be thought of as a schema, which is composed of information from one's own cognitive mechanisms as well as from the external world (Neisser, 1976).

It has been proposed that these internal models make predictions about actions, limb kinematics and parameters of the external world and enable successful planning and execution of movement (Wolpert, 1997). Prediction is a necessary step in motor planning and can be used in many ways, for example, for fine motor adjustments, action planning and motor learning. For every intended action, the brain must issue a motor command to the muscles in order to execute the action. It is proposed that a duplicate of the motor command - or 'efference copy' - is generated in parallel and used to make predictions about the sensory consequences of one's own action (Miall & Wolpert, 1996). Internal forward models are used, for example, to gauge the relationship between predicted states and desired states and to provide the motor instructions required by the muscles to achieve the desired effect, such as the grip force necessary to manipulate a given object (Wolpert et al., 1995). Accurate motor control requires up to date information about the external world. For example, it is only possible to make accurate reaching movements by acquiring an internal model of our limb dynamics. Recently, it has been shown that internal model prediction occurs even in the absence of movement (Voss et al., 2006). Internal models are constantly updated based on the actions and experiences of the person in the world (Miall & Wolpert, 1996; Wolpert et al., 1995). As body kinematics change during adolescence, the representation and prediction of actions made by internal models require updating.

5.2. Motor imagery as a paradigm to study action representation

It has been posited that by studying conscious motor imagery, it is possible to access the unconscious process of action representation (Jeannerod, 1997). Motor imagery is a conscious, first-person simulation of an action, for example, imagining the sensation of generating the force of the leg to kick a football, without actually moving. The conscious generation of a motor image reflects an unconscious internal action representation, or "internal model" of volitional movements (Jeannerod, 1997).

A tight correlation between the timing of a specific action and its imagined equivalent has been shown to be a robust phenomenon, suggesting that actions in both modalities are subject to the same environmental and physiological constraints (Decety & Michel, 1989; Jeannerod, 1994; Sirigu et al., 1995; Wilson et al., 2001). For example, there is no difference in the time taken to carry out or to imagine tasks that involve writing, drawing (Decety & Michel, 1989), walking (Decety et al., 1989; Stevens, 2005), performing simple hand actions, including the "fingers task" employed here (Sirigu et al., 1996), or reaching to targets (Cerritelli et al., 2000; Maruff et al., 1999; Wilson et al., 2001). Furthermore, the visually-guided pointing task (VGPT) has previously been used to show that, typically, the duration of target-oriented reaching movements increases as the size of the target decreases (Cerritelli et al., 2000; Maruff et al., 1999), both when the actions are executed and imagined. In other words, task difficulty, also referred to as the index of difficulty, affects actions in the same way, regardless of modality. Taken together, the temporal invariance between executed and imagined movements suggests that the same motor representation governs an action whether it is executed or imagined.

5.2.1. Fitts' Law

This phenomenon can be expressed by Fitts' Law (Fitts, 1954). This describes the logarithmic relationship between the speed and accuracy of actual movements, and has been shown to extend to imagined movements in typical participants. In other words, we make the same speed-accuracy trade-offs for both executed and imagined actions (Decety & Jeannerod, 1995; Sirigu et al., 1995; 1996). For example, for both executed and imagined movements, we slow down in order to reach accurately to increasingly

small targets, or we take longer to walk to increasingly distant targets (Decety et al., 1989; Maruff et al., 1999; Sirigu et al., 1996; Wilson et al., 2001).

5.2.2. Motor imagery and parietal cortex

In patients with parietal lesions, however, this relationship is lost (Maruff et al., 2003; Sirigu et al., 1996; Wolpert et al., 1998). Impairment in internal models has thus been shown in patients with PC lesions (Sirigu et al., 1996; Wolpert et al., 1998) as well as in schizophrenic patients (Maruff et al., 2003). Together with neuroimaging (Gerardin et al., 2000; Lacourse et al., 2005; Stephan et al., 1995) and electrophysiological experiments (Kalaska & Crammond, 1995), the results suggest that motor imagery is associated with activity in PC. This is supported by the proposal that internal models are stored in PC (Blakemore & Sirigu, 2003; Wolpert et al., 1998).

5.3. Experiments 4A, 4B & 4C: Development of action representation during adolescence

5.3.1. Introduction

It has been proposed that action understanding may be linked to social understanding (see Chapter 1). The development of action representation has not yet been studied in a developmental context beyond childhood and through adolescence. Adolescent development provides an opportunity to study the development of the cognitive basis for action representation and thus to make interpretations about its possible link to higher social cognitive skills. As detailed above 'action representations' are synonymous with internal models of action. In order to maintain accurate motor control, internal models need to be updated in accordance with physical development during this transitional period. Internal models of action have been associated with PC, a region of the brain subject to considerable development during adolescence. Although motor imagery is a well-established phenomenon in healthy adults, the development of this ability during adolescence has not previously been studied. In the following three experiments, three different tasks – in Experiment 4A, the "triple 8 task", in Experiment 4B, the "fingers task"[5] and in Experiment 4C, the "visually-guided point task" (VGPT) – were used to tap internal models in adolescents and adults, and mental chronometry

[5] See Choudhury, S., Charman, T. & Blakemore, S.-J. Development of action representation during adolescence. *Neuropsychologia,* in press

was used as a measure of the ability to represent actions. Three separate motor imagery experiments were conducted firstly, to test whether development of motor imagery ability extends to different types of tasks. These tasks are also amenable to different types of statistical analysis to one another. As an index of the development of the action representation system, we measured the correspondence between the time course of every participant's executed (E) and imagined (I) actions in each age group, on the three different motor imagery tasks. To compare this correspondence between age groups, we compared the Execution-Imagery (E-I) correlations of each individual in the two age groups. To determine whether developmental change was specific to the development of internal models and not a result of general cognitive-motor improvement, the change in E-I correlation with age was compared to the change in general cognitive-motor efficiency with age. In addition, in Experiment 4C, each group's compliance to Fitts' Law was compared.

For Experiment 4A, it was predicted that there would be an 'isochrony effect' for the 'triple 8 task' such that execution and imagery times would be maintained regardless of the size of the 8. This prediction was based on a previous study showing that handwriting time remains constant irrespective of size (Decety & Michel, 1989). It was predicted that in Experiment 4B, there would be an effect of laterality for the 'fingers task', such that the time taken to both execute and imagine actions with the dominant hand would be relatively faster. For Experiment 4C, it was predicted that there would be a main effect of Index of Difficulty (ID), with all participants taking a longer time to reach for the smaller targets (Cerritelli et al., 2000; Maruff et al., 1999; Sirigu et al., 1995; 1996; Wilson et al., 2001), due to the speed-accuracy trade off typically represented. Furthermore, given the pronounced development of body structure and therefore limb dynamics during adolescence, it was hypothesised that forward modelling for action control would show parallel development. It was predicted that this would be reflected by an increase between adolescence and adulthood in the correspondence between Execution and Imagery times in all three experiments.

EXPERIMENT 4A:

5.3.2. Method for Triple 8 task

5.3.2.1. Participants

73 participants were recruited and divided into two age categories. 40 adolescents (24 males; mean age 13.1 years, SD=1.4) and 33 adults (15 males; mean age 27.5 years, SD=7.9). Adolescent participants were from state comprehensive primary and secondary schools in the London area and adults were students and staff at University College London. Participants were all right handed and none had a history of psychiatric, neurological, developmental or learning disorder. Written informed consent was obtained from the participants and, for the adolescents, from their parents prior to the study, which was approved by the local research ethics committee.

5.3.2.2. Experimental procedure

For each trial, participants were presented with a plain sheet of paper. Two parallel horizontal lines were drawn, with one towards the top of the sheet and the other pair towards the bottom. An example of the figure 8 was drawn between the top pair of lines such that its height spanned the width between the lines.

5.3.2.2.1. Executed condition for triple 8 task

Participants sat with their hand in a starting position with the tip of the pencil touching the centre of the X drawn between the bottom pair of lines (See Figure 5.1). When the experimenter said "Go", participants were instructed to draw a further three consecutive figure 8s as fast and as accurately as they could within the bottom pair of lines, without going outside the border of the lines. The width between the lines and therefore the sizes of the figure 8s varied. Three different sizes were used: 70, 35 and 18 mm high. There were three trials of each size of 8, on separate sheets of paper, for the Executed condition and also for Imagined condition. A stopwatch was used to record the duration of participants' movement from the time the experimenter said 'Go' to the time the participant said 'Stop'.

5.3.2.2.2. Imagined condition

The Imagined condition followed the Executed action blocks. During this condition, participants were instructed to place their hands in the starting position for the action (for Exp. 4C this meant holding the pencil at the starting point of the vertical line on

each sheet), but they were asked to keep as still as possible during the Imagined trials. When the experimenter said 'Go,' participants were required to *imagine* doing the action exactly as in the Executed condition, but without moving. As in the Action condition, participants were told to say 'Stop' out loud to indicate they had finished the imagined movements.

5.3.2.2.3. Instructions

Each participant was given a demonstration by the experimenter at the beginning of the task. To ensure that participants had fully understood the instructions, they were given a Practise condition consisting of three example trials which were not included in the main experiment.

In the Imagined condition, the experimenter always stressed that participants should 'really feel themselves making the movement'. In other words, they were to avoid objectifying themselves by imagining a visual image of their hand moving. Rather, they were supposed to feel as if they were actually moving their hand in a first-person perspective of the motor image. If the participant lost count of the number of movements, lost concentration during a trial, or expressed any problems, then that trial was subsequently excluded from the analysis. At the start of every block, for each task, participants were reminded to perform the actions as quickly and as accurately as possible.

During the piloting stage, the order of blocks was counterbalanced between participants, so that some started with the Imagined condition and others with the Executed condition. It was found that starting with the Imagined condition was challenging for subjects, who reported not knowing what to imagine. Therefore, it was decided that, during the actual study, participants would perform the tasks in blocks of Executed actions followed by Imagined actions.

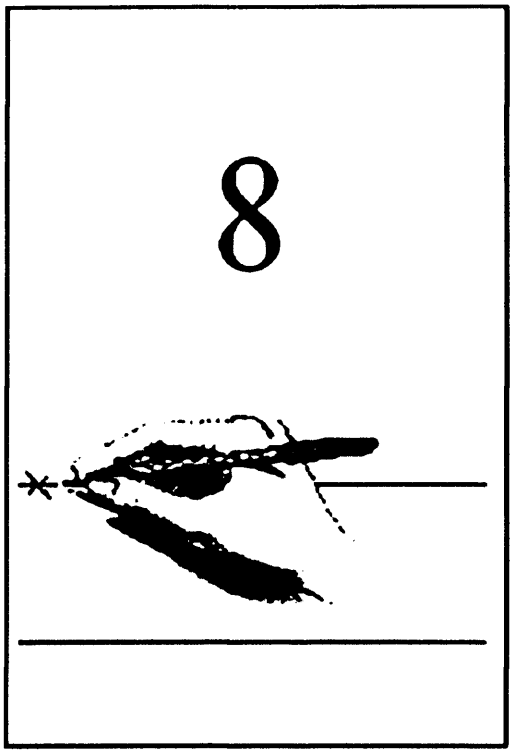

Figure 5.1.*Triple 8 task. Executed (E).* *Participants drew three consecutive figure 8s with a pencil, within the parallel pair of lines, as quickly and as accurately as they could. There were three size conditions of the figure 8: small, medium and large corresponding to varying distances between the parallel lines. They were timed between the time they were instructed to start and the time they said 'stop' to indicate they had finished. Imagined (I). Participants were timed to imagine making this action without moving their hand at all.*

5.3.2.2.4. Praxis Imagery Questionnaire (PIQ)

To check that there was no difference between groups in the ability to image actions, we administered an imagery questionnaire to all participants. The PIQ was adapted from the children's version (Wilson et al., 2001) of the Florida Praxis Imagery Questionnaire (Ochipa et al., 1997) (see Appendix 5). The questionnaire consisted of seven questions in each of four subscales, each designed to test different aspects of praxis imagery: kinaesthetic, body position, action and object imagery. Correct answers indicated that the participant was able to correctly image the action required to arrive at the answer. The questionnaire was used to check for outliers on a group by group basis. This was to ensure that all data analysed were from participants able to carry out praxis imagery. PIQ scores were analysed by subscale (possible range: 0-7) and by total number correct (0-28). High overall scores were indicators of high ability to image actions. This questionnaire is designed to tap both visual and motor representations in separate subscales.

5.3.2.3. Data analysis

5.3.2.3.1. Individual reaction time data for Imagined and Executed actions

For each participant, the mean movement duration for all the trials (nine for the triple 8 task; eight for each condition of the fingers task) under the Executed and Imagined conditions was calculated. To investigate how well these data correlated across participants, each participant's mean Executed RT (E) was plotted against his or her mean Imagined RT (I), for each task. Individual correlations provide information about motor imagery ability, which would be masked by comparing group means. A Pearson's product moment correlation was calculated between the mean E-RT and mean I-RT. In addition E time was compared between groups, as was I time. These measures were used as controls to test whether any development was specific to action representation (as indexed by E-I correlation) and not by general movement or general imagery ability.

5.3.2.3.2. Comparison of E-I correlations between groups

Fisher's Z was used to test whether the size of the correlations between executed and imagined movement duration significantly differed between the age groups and between genders on each task. According to this test, if the Z value was above 1.96, the

correlations were significantly different at the $p<0.05$ level, and if the Z value was 2.58 or over, the correlations were significantly different at the $p<0.01$ level.

5.3.2.3.3. The effect of action size

To investigate the effect of size of the figure 8 in this task, a mixed design 3x2x2 (Size x Age x Gender) ANOVA was used.

5.3.3. Results

5.3.3.1. PIQ for all experiments

All participants scored highly on the PIQ, and there were no differences between groups in the mean total scores or in any of the subscales (mean score (adolescents) = 24; mean score (adults) = 26 out of a total of 28; see Table 5-1). A participant's imagery and action data were excluded from the analysis if his or her mean PIQ score fell three or more standard deviations below the mean score from his or her age group. One adolescent's data fell into this category. This analysis indicated that all participants whose data were included in subsequent analyses were able to form all aspects of imagery tapped by the PIQ which included both visual and motor representations.

SUBSCALE	ADOLESCENTS			ADULTS		
	Mean±S.D.	Median	Range	Mean±S.D.	Median	Range
Kinaesthetic	5.2±0.99	5	2-7	5.2±1.1	5	3-7
Position	6.3±0.82	6	3-7	6.6±0.56	7	5-7
Action	6.3±0.88	6	4-7	6.7±0.64	7	4-7
Object	6.4±0.79	7	4-7	6.6±0.55	7	5-7
Total	24.2±0.54	24		25.1±0.74	26	

Table 5-1. *PIQ scores. The table indicates the mean, median and range of scores for each subscale. There were no differences between age groups in Imagery questionnaire scores, indicating that both adolescents and adults were able to image actions correctly. The questionnaire was used to identify and exclude data from participants whose scores fell 3 S.D. below the mean score for each group.*

5.3.3.2. Action imagery tasks

Participants who showed a discrepancy between imagined and executed action times that were three standard deviations above or below the mean in either of the two tasks were also considered outliers. There were two outliers for the Triple 8 task (one adult and one adolescent).

5.3.3.2.1. Execution-Imagery (E-I) correlations

The correlation between the timing of actual (E) and imagined (I) actions was significant for both age groups (R^2 (adolescents)=0.58; R^2 (adults)=0.87; $p<0.01$ for both). However, the correlation between E and I for individuals in the adult group was significantly higher than that of individuals in the adolescent group ($Z=2.61$; $p<0.01$). There was no effect of gender on either the executed or imagined conditions (Z(adolescents)=1.10; Z(adults)=0.17). Thus, performance on both tasks indicated that the ability to form accurate action representations, as indexed by the strength of the correlation between executed and imagined actions, significantly improves between early adolescence and adulthood (see Figure 5.2).

5.3.3.2.2. Relationship between action time and age

The second set of regression analyses (see Figure 5.3) revealed no significant correlation between age and movement execution time (E) for the Triple 8 task ($R^2=2.9\text{x}10^{-4}$; $p=0.89$). This indicates that both age groups performed the motor execution task equally efficiently. Similarly, there was no significant correlation between age and imagery time (I) for this task ($R^2=0.044$; $p=0.082$) (See Figure 5.3). These control regression analyses show that there was no difference between age groups in terms of motor speed and other general factors such as understanding task instructions, making a hand action, and reaction time. There were no differences between genders in either the E or I condition.

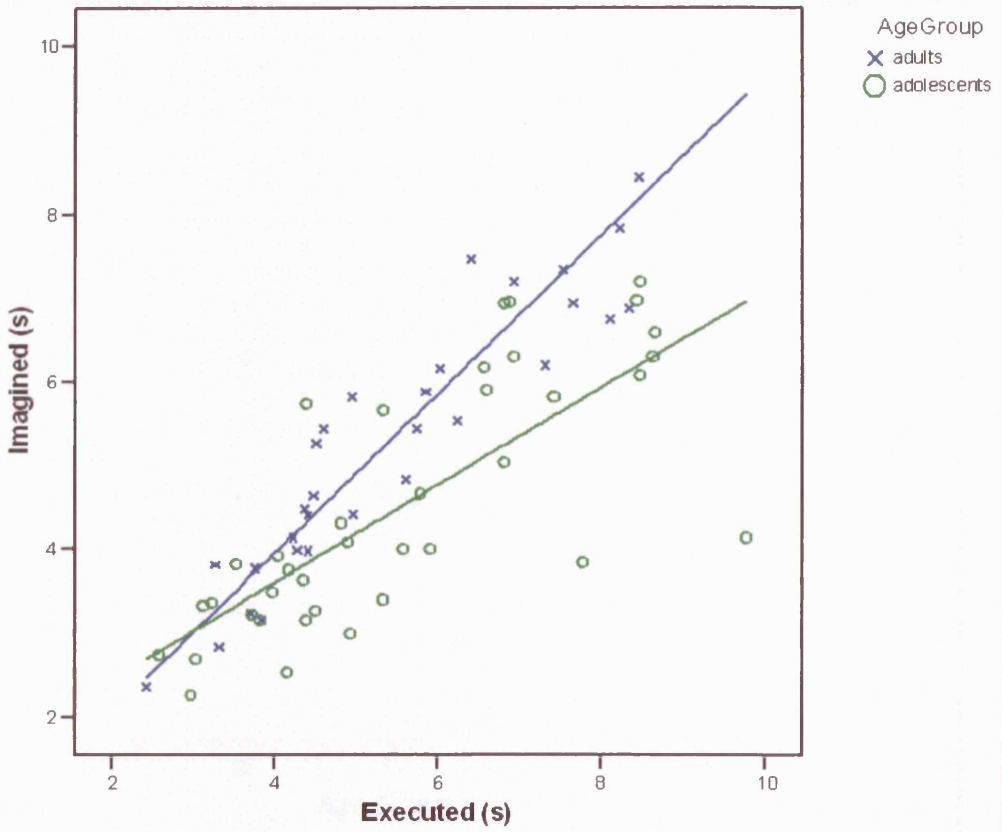

Figure 5.2. Triple 8 task E-I correlation. *Graph shows a significantly greater E-I correlation for adults (R^2=0.867) than for adolescents (R^2=0.58), p<0.01*

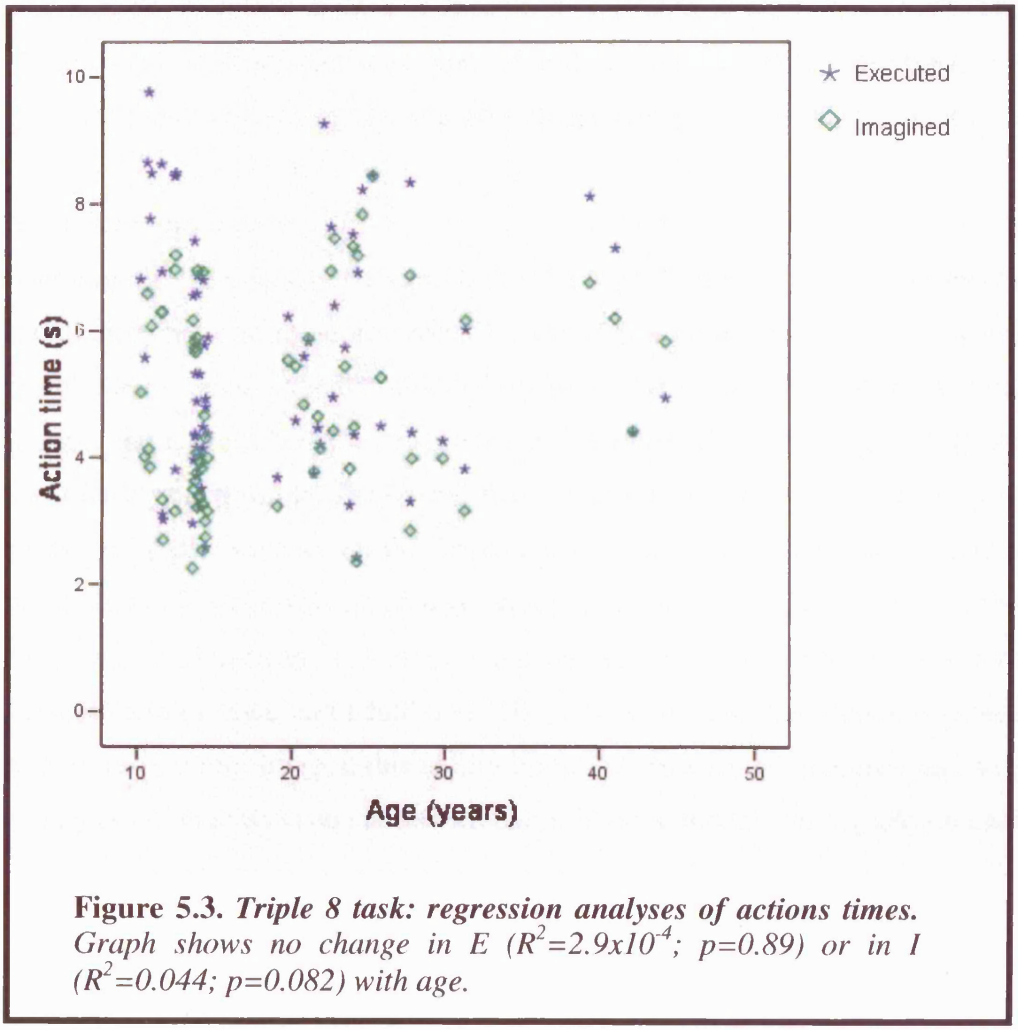

Figure 5.3. ***Triple 8 task: regression analyses of actions times.*** *Graph shows no change in E (R^2=2.9x10^{-4}; p=0.89) or in I (R^2=0.044; p=0.082) with age.*

5.3.3.2.3. Size of action (Figure 8 task)

There was a main effect of Size of Action (handwriting size) ($F(2,64)=84.3$; $p<0.0001$), indicating that on average across both the I and E trials participants performed the actions increasingly slowly as the size of the figure 8 increased (mean RT for small 8=4.32s, SE=0.16; medium 8=5.16s, SE=0.21; large 8=6.26s, SE=0.27). There was a significant interaction between Size of Action and Age ($F(2,130)=6.83$; $p<0.01$) but post-hoc t-tests comparing RT of each size between groups were not significant.

5.3.4. Mini discussion

This experiment employed a novel task – the triple 8 task – to assess the development of motor imagery during adolescence. This task was designed to involve a fluid action, which did not have a metronomic quality to it. The results showed that within both age groups, the correlation between timing of Executed (E) and Imagined (I) actions was significant and positive, suggesting that the ability to accurately represent actions, as reflected by performance on the Triple 8 task, is in place in adolescents and adults. In addition, while there was no change with age in the E-time *per se* or the I-time *per se*, there was a significant increase in the degree of correspondence between E and I between adolescence and adulthood. These data indicate that although adolescents are able to form motor images, this ability improves between adolescence and adulthood. It is suggested that this is due to refinement of internal models during adolescence.

EXPERIMENT 4B:

5.3.5. Method for Fingers task

5.3.5.1. Participants

See details of Experiment 4A above. The same adolescent and adult groups participated in this experiment.

5.3.5.2. Experimental procedure

Each participant was seated in a quiet room with the experimenter, with his/her right arm raised from the elbow and palm facing his/her face. During the piloting stage, the order of blocks was counterbalanced between participants, so that some started with the Imagined condition and others with the Executed condition. We found that starting with the Imagined condition was challenging for subjects, who reported not knowing what to imagine. Therefore, it was decided that, during the actual study, participants would perform the tasks in blocks of Executed actions followed by Imagined actions.

5.3.5.2.1. Executed condition for Fingers task

The fingers task was identical to that described by Sirigu et al. (1996). Two blocks of Executed actions were followed by two blocks of Imagined actions, with each block consisting of a sequence of five consecutive, continuous actions.

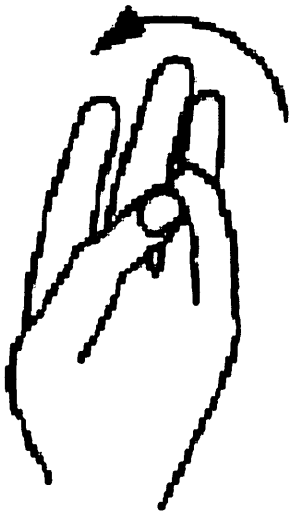

Figure 5.4. ***Fingers task****. Executed (E). Participants moved their thumb between their little finger and index finger in a continuous sequence of five movements, as quickly and as accurately as they could. They were timed between the time they were instructed to start and the time they said 'stop' to indicate that had finished. This was repeated with both the right and left hands. Imagined (I). Participants were timed to imagine making this action without moving their hand at all.*

When the experimenter said 'Go,' participants were required to touch the right thumb to the tip of the little finger and then to the tip of the index finger (See Figure 5.4). In each block, this action was repeated five times (one sequence was equivalent to the thumb touching both the little finger and the index finger; this whole motion was repeated five times as one repetitive continuous motion). Participants were instructed to say 'Stop' to indicate that they had completed the sequence of actions. In half of the blocks, participants used their right hand and in the other half of the blocks, their left hand. The experimenter used a stop-watch to time the duration of the action from the moment after she said 'Go' to the moment the participant said 'Stop'.

5.3.5.2.2. Imagined condition

See Method section 5.3.2.2.2 from Experiment 4A.

5.3.5.2.3. Instructions

See Method section 5.3.2.2.3 from Experiment 4A.

5.3.5.2.4. Praxis Imagery Questionnaire (PIQ)

See Method section 5.3.2.2.4 from Experiment 4A.

5.3.5.2.5. Data analysis

See Method section 5.3.2.3.1 and 5.3.2.3.2.

5.3.5.2.6. The effect of laterality

Group means of RT were analysed using a between-subjects 2x2x2 (Hand x Age x Gender) ANOVA to explore laterality for the fingers task. The effect of laterality for this task was also analysed by comparing E-I correlation for the left and right hand within each age group.

5.3.5.3. Results

There were two outliers for the Fingers task (two adults).

5.3.5.3.1. PIQ

There were no differences between age groups in any of the subscales of the PIQ. See Results section 5.3.3.1 in Experiment 4A for details.

5.3.5.3.2. E-I correlations

The correlation between E and I were also significant for both age groups (R^2 (adolescents)=0.82; R^2 (adults)=0.96; $p<0.01$ for both). Again, the correlation between E and I for individuals in the adult group was significantly higher than that for individuals in the adolescent group ($Z=3.20$; $p<0.01$). There was no effect of gender (Z(adults)=0.492; Z(adolescents)=1.24). In line with the results from the first task, performance on the Fingers task indicated that the ability to form accurate action representations significantly improves between early adolescence and adulthood (see Figure 5.5).

5.3.5.3.3. Relationship between action time and age

The second set of regression analyses (see Figure 5.6) revealed no significant correlation between age and movement execution time (E) for the Fingers task ($R^2=0.041$; $p=0.1$).

Similarly, there was no significant correlation between age and imagery time (I) for the Fingers task ($R^2=0.042$; $p=0.1$). Again, these control regression analyses show that there was no difference between age groups in terms of carrying out a motor execution task, and other general factors such as understanding task instructions, making a hand action, and reaction time. There were no differences between genders in either the E or I condition.

5.3.5.3.4. Laterality (Fingers task)

The ANOVA revealed no effect of the hand used for the Fingers action on RT ($F(1,64)=0.34$; $p=0.55$). There was no interaction between Hand and Age Group ($F(1,64)=0.53$, $p=0.47$ or between Hand and Gender ($F(1,64)=0.15$, $p=0.70$)). Furthermore, a comparison between E-I correlations for each hand showed no difference in strength of the E-I association between hands for adolescents or (R^2(left hand)=0.79; R^2(right hand)=0.82; $Z=0.44$, *n.s.*) or for adults (R^2(left hand)=0.94; R^2(right hand)=0.92; $Z=0.54$, *n.s.*).

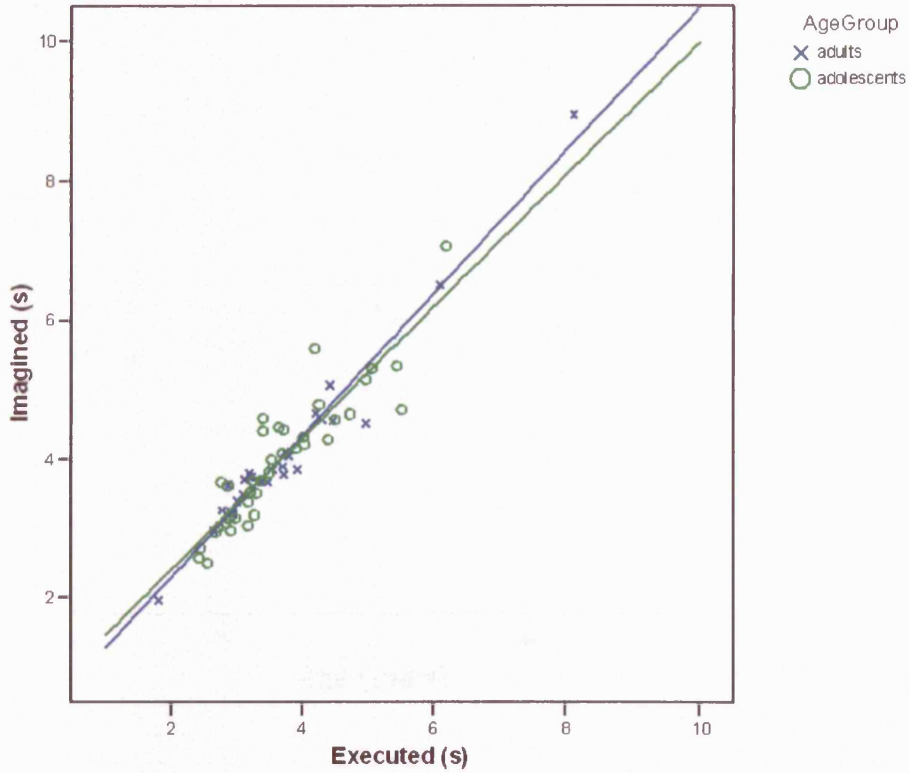

Figure 5.5. Fingers task E-I correlation. *Graph shows a significant increased E-I correlation for adults (R^2=0.958) compared with adolescents (R^2=0.818), p<0.01*

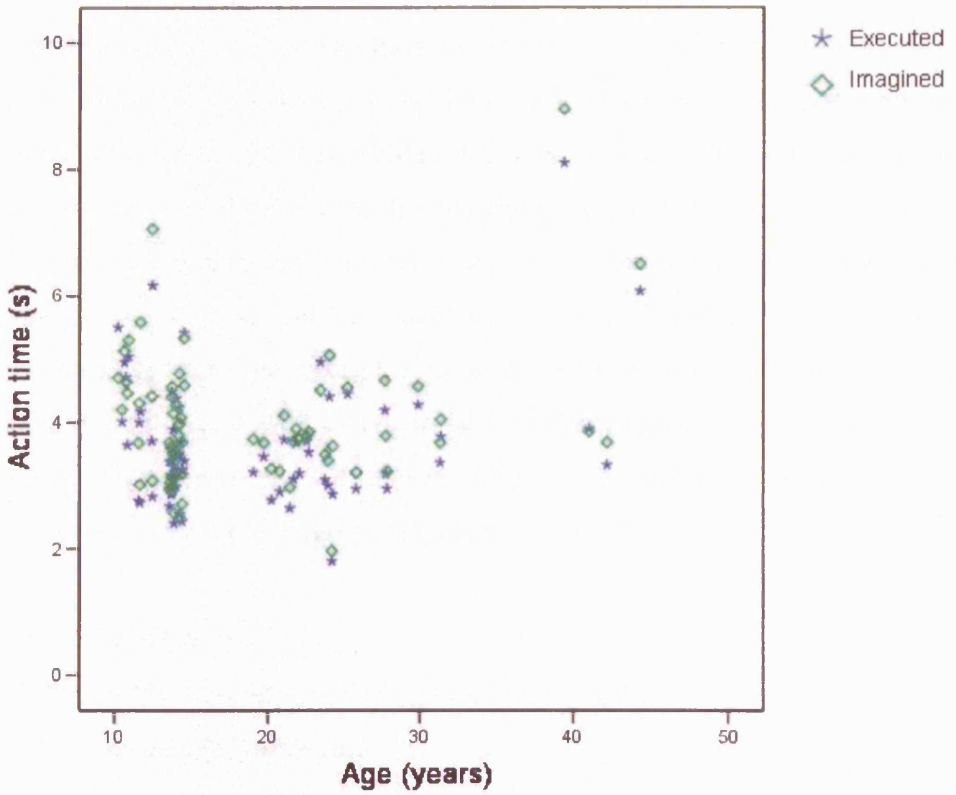

Figure 5.6. ***Fingers task: regression analyses of action times.*** *Graph shows no change in E (R^2=0.041; p=0.1) or in I (R^2=0.042; p=0.1) with age.*

5.3.6. Mini discussion

This experiment replicated a task – the fingers task – from a previous experiment used with healthy adults and adult patients with parietal lesions (Sirigu et al., 1996) to assess the development of motor imagery during adolescence. This task has a periodicity or rhythmic quality to it. The results showed that within both age groups, the correlation between timing of Executed (E) and Imagined (I) actions was significant and positive, in line with results from Experiment 4A. Again, this suggests the ability to represent accurately actions, as reflected by performance on the Fingers task, is in place in adolescents and adults. In addition, while there was no change with age in the E time *per se* or the I time *per se*, there was a significant increase in the degree of correspondence between E and I between adolescence and adulthood. These data indicate that although adolescents are able to form motor images, this ability improves between adolescence and adulthood. Thus, a second type of motor imagery task suggests a refinement of internal models during adolescence.

EXPERIMENT 4C:

5.3.7. Method for visually-guided pointing task (VGPT)

5.3.7.1. Experimental procedure

5.3.7.1.1. Executed condition

The VGPT was adapted from that used by Sirigu et al. (1995, 1996). Participants were required to use their right hand for every trial. For each trial, participants were presented with a plain sheet of paper. On the left hand side of the paper, an 80 mm vertical line was printed and to the right side of it, a black target box with its closest edge 30 mm away from the line (see Figure 5.7). Five different sheets were used and on each sheet the widths of the target box were 3.0, 5.3, 10.6, 18.9 and 28 mm. The order of administration of the different sized targets was counterbalanced between participants. For each trial of a single target width, participants made five hand movements, where one movement was defined as each participant's hand motion (in both the executed and imagined condition) from the far side of the vertical line to touch the target and back to the far side of the vertical line. Participants were told that they could touch the pencil down anywhere inside the borders of the target square. A stopwatch was used to record the duration of participants' hand movements. For the executed condition, participants completed two trials of each of five target widths giving a total of 10 trials per participant. The action was timed from the moment the experimenter said "Go" until the

participant made the fifth movement back to the far side of the line and said "Stop" out loud.

5.3.7.1.2. Imagined condition

See Method section 5.3.2.2.2 from Experiment 4A.

5.3.7.1.3. Instructions

See Method section 5.3.2.2.3 from Experiment 4A.

5.3.7.1.4. Praxis Imagery Questionnaire (PIQ)

See Method section 5.3.2.2.4 from Experiment 4A.

5.3.7.2. Data analysis

5.3.7.2.1. E-I correlations

See Method section 5.3.2.3.1

5.3.7.2.2. Relationship between action time and age

See Method section 5.3.2.3.2.

5.3.7.2.3. Fitts' Law analysis

To investigate whether the same constraints were operating on action representations of both adolescents and adults, performance on the VGPT was analysed using an established method specifically for this type of pointing task. This method determines how well movements performed by both groups conformed to Fitts' Law. The mean movement duration for each group was plotted against target width for each condition. Each target width was also converted to an Index of Difficulty (ID) using the Fitts' Law equation as below:

$$\text{Index of Difficulty (ID)} = \text{Log}_{10}[2 \times A/W],$$

where A is the amplitude of the movement (a constant value of 30mm) and W is the width of the target square. A logarithmic and linear curve was fitted to the data points and a least squares calculation was used to determined the goodness of fit for each curve (Maruff et al., 1999, Sirigu et al., 1995; Wilson et al., 2001).

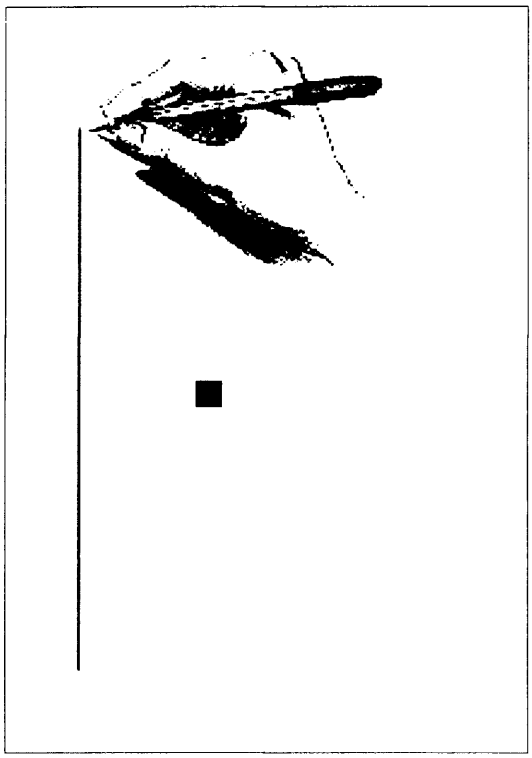

Figure 5.7. ***Visually guided pointing task.*** *Participants were required to move, and to imaging moving, a pencil from the starting point at the top of the line to anywhere within the target square and back again as quickly and as accurately as possible.*

5.3.7.2.4. Group reaction time for Item Difficulty

To investigate the effect of Item Difficulty (ID) (5 levels), a reflection of size of target, on movement duration, a repeated measures 5 (ID) x 2 (age group) x 2 (gender) ANOVA was used to test the hypothesis that participants in both groups would get progressively slower as the target object size decreased, in line with Fitts' Law (Cerritelli et al., 2000; Maruff et al., 1999; Wilson et al., 2001).

5.3.7.2.5. Individual correlations for each participant

A correlation between the timings for each of the 25 single E movements and 25 I movements was calculated for every subject. Individual R^2 values were then compared across age groups.

5.3.8. Results

There were two outliers (one adult and one adolescent) for the VGPT.

5.3.8.1. Group data for Item Difficulty (ID)

A between subjects repeated measures 2 (age group) x 5 (ID) x gender (2) ANOVA showed that there was a main effect of ID ($F(4,64)=29.7$; $p<0.0001$), indicating that on average across both the I and E trials, participants in both age groups performed the actions increasingly efficiently as the target size increased (mean RT + SE for ID 1.3 (3.0mm)=4.95±0.14s,; RT for ID 1.05 (5.3mm)=4.73±0.14s; RT for ID 0.75 (10.6mm)=4.45±0.13s, RT for ID 0.5 (18.9mm)=4.22±0.13s; RT for ID 0.33 (28mm)=4.04±0.13s). See Figure 5.8. There were no effects of age ($F(1,67)=2.72$, $p=0.104$) or gender ($F(1,67)=0.01$, $p=0.979$).

5.3.8.2. Fitts' Law analysis of group means

The established logarithmic relationship between the speed and accuracy of executed movements (Fitts' Law) extended to all age groups and also to the imagined condition for all age groups. The linear relationships between Index of Difficulty (ID) and movement duration that arose from the Fitts' Law equation are shown in Figure 5.9. Table 5-2 indicates that for both adults and adolescents, the logarithmic regression provided the best fit of the data for the actual and imagined conditions when plotted against target width. For both groups, the data conformed highly significantly to Fitts' Law.

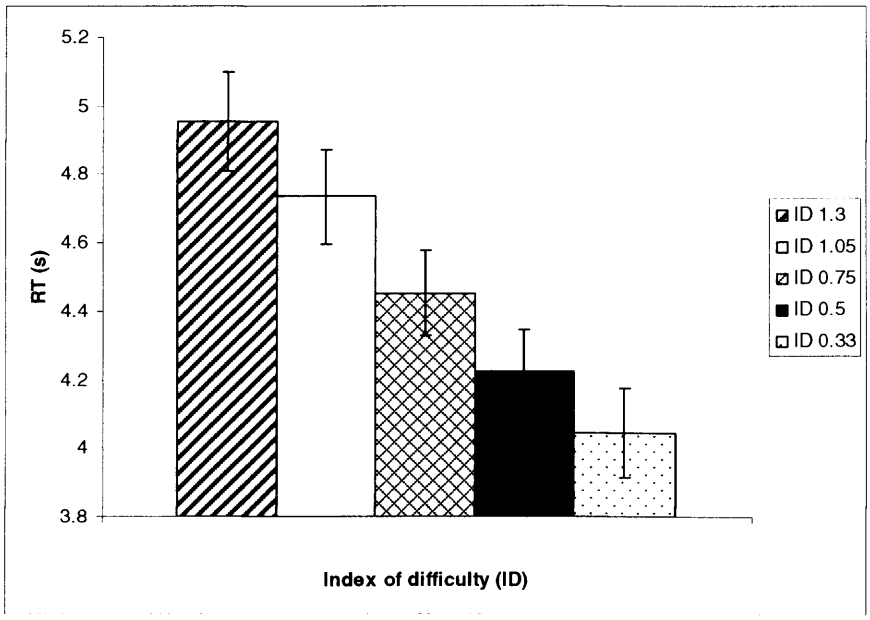

Figure 5.8. ***Mean movement duration ± S.E. as a function of Index of Difficulty (ID).*** *As ID decreaseD (or target size increased), movement duration decreased in line with Fitts' Law, among all participants.*

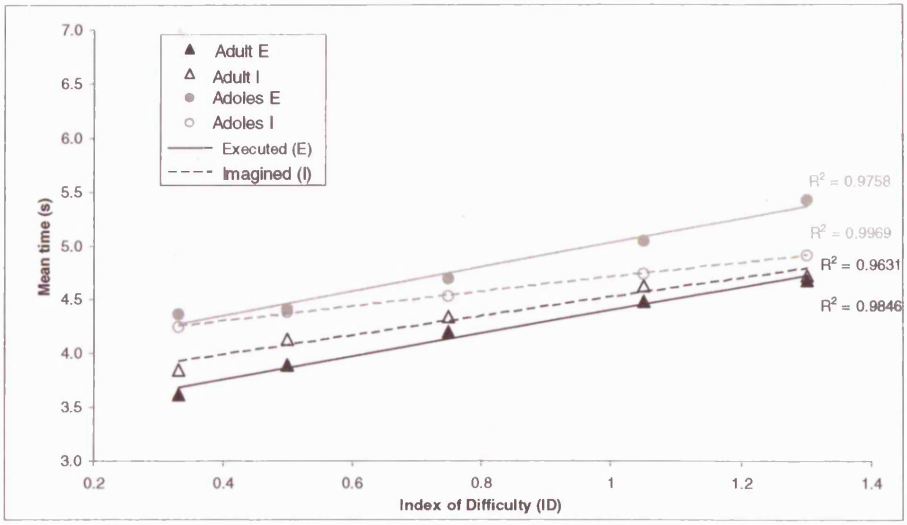

Figure 5.9. ***Fitts' Law analysis for each age group****. The graph shows the linear relationships between Index of Difficulty (ID) and movement duration that arose from the Fitts' Law calculations. Movements of all age groups conform strongly to Fitts' Law.*

Group / condition	Logarithmic	R^2	Linear	R^2
Adolescents				
Executed	$y = -0.488\text{Ln}(x) + 5.89$	*0.975***	$y = -0.040x + 5.30$	*0.817**
Imagined	$y = -0.292\text{Ln}(x) + 5.22$	*0.997****	$y = -0.025x + 4.88$	*0.916**
Adults				
Executed	$y = -0.467\text{Ln}(x) + 5.24$	*0.985****	$y = -0.041x + 4.71$	*0.973***
Imagined	$y = -0.383\text{Ln}(x) + 5.21$	*0.964***	$y = -0.034x + 4.78$	*0.983****

Table 5-2: ***Fitts' Law analyses.*** *The table shows the equations for both logarithmic and linear regressions of mean movement duration against ID. R^2 values for both ages show that E and I movements of both groups conform highly to Fitts' Law. [*** $p < 0.001$; ** $p < 0.005$; * $p < 0.05$]*

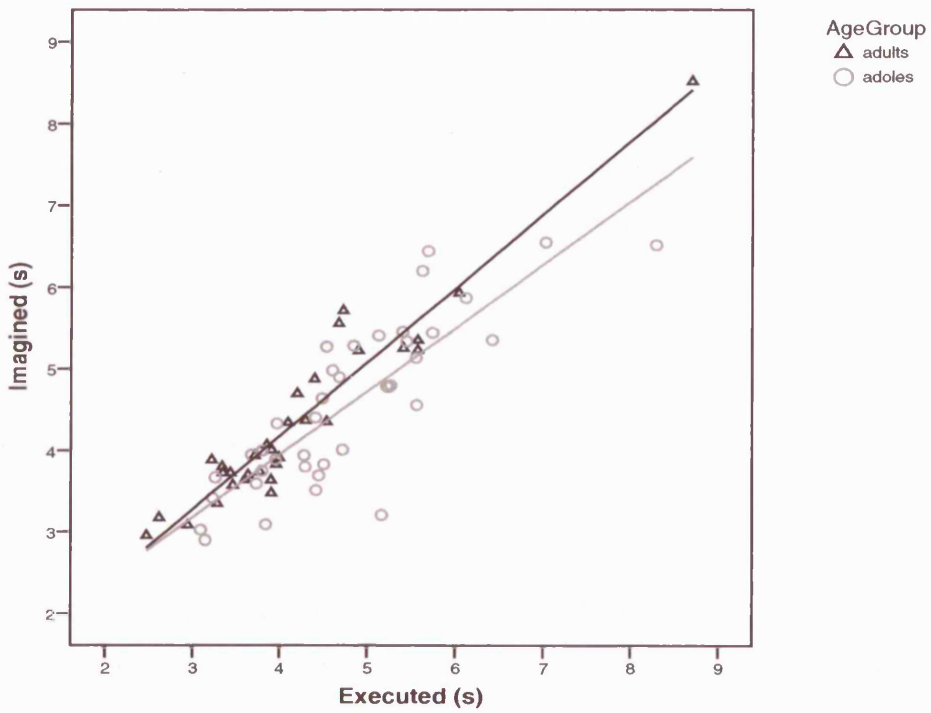

Figure 5.10. ***E-I correlations for each group.*** *Correlations are significant for adolescent and adult group (adults: R^2=0.914; p<0.01; adolescents: R^2=0.698; p<0.01);. E-I correlation for adults is significantly higher than that of adolescents (Z=2.93; p<0.01).*

5.3.8.3. E-I correlations

5.3.8.3.1. Within-group correlations between E and I

The correlation between the timing of E and I was significant for both adults (R^2=0.914; p<0.01) and adolescents (R^2=0.698; p<0.01; see Figure 5.10).

5.3.8.3.2. Between-group comparison of E vs. age and I vs. age

A regression of movement time, in both E and I modalities, over age as a continuum, showed that neither Execution time nor Imagery time *per se* changed as a function of age (E vs. age: $R^2 = 1.0 \times 10^{-5}$, *n.s.*; I vs. age: $R^2 = 0.01$, *n.s.*).

5.3.8.3.3. Between-group comparison of E-I correlations

However, the correlation between E and I of the adult group was significantly higher than that of the adolescent group (Z'=2.93; p<0.01) as shown in Figure 5.10.

5.3.8.3.4. Individual correlation data between E and I

In addition, individual participants' correlation data demonstrated that adults tended to have a higher correlation between E and I than adolescents on an individual-by-individual basis ($\chi^2(1,71)=8.6$, p<0.005). In the adult group, a higher proportion (75%) of individuals had R^2 (E/I) >0.5 than in the adolescent group (44%).

5.3.9. Mini discussion

This experiment replicated a task – the VGPT task – from a previous experiment used with adults (Sirigu et al., 1995; 1996) and children with developmental coordination disorder (DCD) (Maruff et al., 1999) to assess the development of motor imagery during adolescence, using a third task. This task involves a visually-guided pointing action. The results demonstrate that within both age groups, the correlation between timing of Executed (E) and Imagined (I) actions was significant and positive, suggesting the ability to represent accurately actions is in place in adolescents and adults. Similarly, as reflected by the effect of Index of Difficulty (ID) on movement duration as well as least squares regressions, actions in both E and I conditions conformed highly significantly to Fitts' Law in both age groups However, as in Experiments 4A and 4B, again there was a significant increase in the degree of correspondence between E and I between adolescence and adulthood. These data from the third motor imagery task used

in this thesis indicate that both adolescents and adults are able to form motor images, but this ability improves between adolescence and adulthood. The data from all of the three experiments are discussed in greater detail below. It is concluded that the replicated findings suggest that this is due to refinement of internal models during adolescence.

5.3.10. General discussion

5.3.10.1. Both adolescents and adults are able to generate motor images

The FPIQ data showed no differences in performance between imagery subscales, indicating both groups were equally able to generate both visual and kinaesthetic representations. To ensure that imagined actions were "felt actions", or first person simulated actions, participants were instructed to imagine themselves as the agent of the action in the Imagery conditions. Moreover, when retrospectively asked about their strategy, participants reported using a motor strategy as instructed. Furthermore, the high correlations between E and I in both groups corroborate results from previous psychophysical experiments, supporting the notion that there are parallels between the parameters affecting executed and imagined movements for both adults and adolescents (Decety & Jeannerod, 1995; Decety & Michel, 1989; Sirigu et al., 1995; 1996).

5.3.10.2. E-I correlation in each age group

Furthermore, the high correlations between E and I in both age groups for all three tasks corroborate results from previous psychophysical experiments (Decety et al., 1989; Decety & Michel, 1989; Jeannerod, 1994; Sirigu et al., 1995), supporting the notion that there are parallels between the parameters affecting executed and imagined movements. This indicates that the Imagery conditions for both tasks were tapping action representations in both adults and adolescents. This correspondence between E and I is explained by Fitts' Law, a model of human psychomotor behaviour, which expresses the relationship between movement time and task difficulty (Fitts, 1954), a phenomenon that has been found to extend to imagined actions as well (Decety & Jeannerod, 1995; Sirigu et al., 1995; 1996). It reflects the finding that subjects make the same speed-accuracy trade-offs for both executed and imagined actions, for example, by slowing down in order to reach accurately to increasingly small targets, or by taking longer to walk to increasingly distant targets (Decety & Jeannerod, 1995; Maruff et al., 1999; Sirigu et al., 1995; 1996; Stevens, 2005). Unlike the study by Maruff et al., (1999),

results of the Fingers task indicate that performance is not influenced by laterality for either of the age groups.

5.3.10.3. Conformity to Fitts' Law in both age groups

As illustrated by the goodness-of-fit regressions in the results of Experiment 4C (Table 5-2 and Figure 5.9), movements in both the E and I conditions of the VGPT tightly conform to Fitts' Law. This suggests that the action representation system is well established in both participant groups. In line with this, the ANOVA revealed a main effect of ID (see Figure 5.8), but no effect of age group, on movement duration. The amplitude of the movement was constant, given that all participants started the movement from the same starting point and aimed for the closest point within the box since they were told to move as quickly as possible. Speed therefore increased with decreasing size. As ID increased (as target width decreased), both adolescent and adult participants were able to represent speed-accuracy constraints such that they slowed down as target size decreased in order to perform actions with accuracy. Furthermore, the correlation between E and I was highly significant for both groups in all three tasks.

This correspondence between E and I is explained by Fitts' Law, a model of human psychomotor behaviour, which expresses the relationship between movement time and task difficulty for both executed actions and imagined actions (Fitts, 1954). It reflects the finding that subjects make the same speed-accuracy trade-offs for both executed and imagined actions (Decety et al., 1989; Maruff et al., 1999; Sirigu et al., 1996; Stevens, 2005).

In addition, we did not find an isochronous effect for handwriting size in the Triple 8 task. A handful of previous studies have shown that participants have a tendency to keep execution time constant independent of movement size (Decety & Michel, 1989; Viviani & McCollum, 1983). The tangential velocity correlates with the trajectory such that movement time tends to remain constant irrespective of size. However, the Triple 8 task was designed to constrain the movement by the lines within which the Figure 8s were restricted. In contrast, in studies where the Isochrony Principle held true, writing movements were "free", e.g. a signature (Decety & Michel, 1989; Viviani & McCollum, 1983). Free movements such as a signature enable the use of one's own unique style of movement and therefore the tagential velocities particular to individual

handwriting. In the current study, however, the participant's velocity is more controlled with respect to the target lines. Our figure of 8 task thus involves accuracy and is therefore perhaps still subject to the Fitts' law effect of timing and movement trajectory.

5.3.10.4. Refinement of internal models during adolescence

The comparison of strength of correspondence between E and I between the two age groups for all three tasks suggests that refinement of this system occurs during adolescence. The statistical comparison indicated that the strength of the E-I correlation is significantly higher among adults than it is in adolescents. Given that there was no difference between groups in the FPIQ scores, the increase in correspondence between E and I indicates that the refinement is specific to the ability to represent the speed and accuracy constraints involved in actions, and not a general development in imagery.

Similarly, the developmental change was specific to motor imagery and was not a consequence of general cognitive-motor improvement. The second set of regression analyses revealed no significant correlation between movement execution time (E) and age for any of the three tasks. This indicates that both age groups performed the motor execution tasks equally efficiently. Similarly, there was no significant correlation between age and imagery time (I) for any of the tasks. This suggests that the developmental effect (an increase in the correlation between E and I with age) is specific to the ability to form accurate motor images based on internal models of action, rather than the ability to perform or imagine movement *per se*. These control regression analyses show that there was no difference between age groups in terms of carrying out a motor execution task, and other general factors such as understanding task instructions, making a hand action, and reaction time.

5.3.10.5. Internal models in the brain

It has long been suggested that the mental processes that contribute to the covert simulation of an action are also involved in the actual performance of that action (Binet, 1885; Stricker, 1885). William James, for example, argued in his ideomotor theory of action that "every mental representation of a movement awakens to some degree the actual movement which is its object" (James, 1890). Motor imagery studies using walking, writing, drawing and simple hand action tasks in normal adults (Decety & Jeannerod, 1995; Decety & Michel, 1989; Sirigu et al., 1995; 1996)) indicate that the

same motor representation governs an action whether it is executed or imagined, and time constraints operate in the same way in both modalities of action.

It is thought that motor imagery might be analogous to efference copy (Decety et al., 1989; Jeannerod, 1997). Efference copy is generated by the brain in parallel with every motor command, and is believed to be crucial to action planning (Wolpert et al., 1995). Internal models make predictions of the consequences of actions on the basis of efference copy (Wolpert et al., 1995). Lesion studies (Sirigu et al., 1996; Wolpert et al., 1998), neuroimaging studies (Stephan et al., 1995) and electrophysiology studies (Kalaska & Crammond, 1995) suggest that the PC is involved in storing and updating internal models of actions, including monitoring efference copy received from motor outputs. Data from motor imagery studies of parietal lesion patients indicate that imagined actions do not follow Fitts' Law, and as such, they are unable to form accurate internal representations of actions (Sirigu et al., 1996; Wolpert et al., 1998). Similarly, children with developmental coordination disorder (DCD) have been shown to demonstrate weaknesses in their action representation system (Maruff et al., 1999). It has been proposed that a weak correlation between executed and imagined actions is due to an "impaired ability to process efferent copy signals" and that the problem may have its origin in the neural circuitry underlying internal models (cf. Maruff et al., 1999, pp. 1323).

5.3.10.6. Development of the brain and internal models during adolescence

In light of several neurophysiological and lesion studies of motor imagery (Gerardin et al., 2000; Lacourse et al., 2005; Sirigu et al., 1995; 1996; Stephan et al., 1995), a speculative interpretation of the current results is that the development in motor imagery found in this study may be linked to the maturational processes in the PC. During the last decade, neuroimaging studies have shown that cortical development is much more protracted than previously believed. Structural MRI studies have demonstrated grey and white matter development in the PC throughout adolescence, which may reflect synaptic pruning and myelination during this period (Gogtay et al., 2004; Sowell et al., 2003; Toga et al., 2006). Given that myelin speeds up neural signalling and synaptic pruning is essential for the fine-tuning of functional networks of brain tissue, the occurrence of these processes in the brain during adolescence should lead to increased neural efficiency (Huttenlocher, 1979; Sowell et al., 1999). Within this context, there

are two possible explanations for the increasing ability to form motor images with age, observed in the current study. Firstly, the maturational processes in parietal circuitry may give rise to an increased ability to process efference copy signals with age, during adolescence. Thus, increased myelination and synaptic pruning in PC could account for the improvement in motor imagery. A second explanation could be that during adolescent growth, internal models are refined such that motor predictions take account of new hand size and dynamics. This may be a consequence of developmental change in the neural networks supporting internal models.

In addition to the PC, histological and MRI data have provided evidence for considerable development in PFC during adolescence (Gogtay et al., 2004; Huttenlocher, 1979; Sowell et al., 2003; Toga et al., 2006). It is possible that the increase in correspondence between imagined and executed timings of actions results from an improvement in working memory that is linked to the maturation of the PFC. Indeed the refinement of internal models reflected by the current data may result from the development and plasticity of frontal and parietal circuitry and reciprocal connections with the cerebellum, a brain region additionally linked to internal models (Blakemore & Sirigu, 2003). Future studies are necessary to determine the differential involvement of cortical circuits in motor imagery for adolescents compared with adults.

Studies of the development of grip force modulation suggest that internal models are established between the ages of four and six (Blank et al., 1999; 2000; Paré & Dugas, 1999). However, none has investigated the development of internal models during the transition from childhood into adulthood. The results above fit with a previous study that compared children (aged between seven and 11 years) and adults on a force adaptation paradigm. This showed that internal representations of arm dynamics were less precise in children and less stable in time than those of adults (Konczak et al., 2003).

5.3.11. Conclusion

These data suggest that development of action representation continues beyond childhood, possibly in response to physical changes in the body during the transition into adulthood, and facilitated by cortical development in the brain. Given that body shape is subject to considerable development during puberty and adolescence, neural

representations of limb dynamics and therefore predictions for actions might be less accurate in adolescents than in adults. If limb kinematics change, due to changed body size, the representation and prediction of actions made by internal models need to be updated on the basis of experience with the new body shape. Refinement of internal models may be supported by the maturation of PC during adolescence. The notion that the action representation system is still developing during adolescence has consequences for the understanding of the typical development of control of thought and action, and may have implications for understanding motor impairment in developmental disorders such as DCD and autism.

The next experiment compares action representation in typically developing adolescents and adolescents with autism spectrum disorders.

CHAPTER 6

6. ACTION REPRESENTATION IN ADOLESCENTS WITH AUTISM SPECTRUM DISORDER

6.1. The autistic phenotype

Autism is a pervasive developmental disorder, which is characterised by difficulties in social communication and social interactions as well as unusual patterns of repetitive behaviour (Wing & Gould, 1979). This 'triad of impairments' forms the basis of the criteria for classification of autism according to DSM-IV-TR (APA, 2000) and ICD-10 (WHO, 1992). Although not part of the diagnostic criteria, problems with motor control are often characteristic of autism as well (e.g. Berkeley et al., 2001; Provost et al., *in press*). Autism is viewed as a spectrum of disorders with childhood autism, Asperger's syndrome (AS) and Pervasive Developmental Delay – Not Otherwise Specified (PDD-NOS) on the same continuum (Gillberg & Gillberg, 1989). Within this continuum are also individuals with below average IQ (<70) ('low-functioning autism') and average or above-average IQ (>70) ('high-functioning autism'). Individuals with AS do not suffer from intellectual disability or language delay but do manifest problems in social reciprocity, social communication and repetitive behaviour patterns. The prevalence of autism spectrum disorders (ASD) in a population cohort of 56,946 children aged nine to 10 years in South London has recently been estimated at 116.1 per 10,000 (over 1%). This study indicated that the prevalence of ASD is 3.3 times higher in boys than in girls (Baird et al., 2006).

Behaviourally, the triad of impairments associated with ASD is manifest in varying degrees. Social communication problems can be verbal and non-verbal and can be characterised by difficulties in pragmatic aspects of communication, such as inappropriate facial expressions or use of eye contact, or problems with gestures (cf. Baron-Cohen, 1999). Social interaction difficulties are seen in peer interactions, in the inability to detect social cues like eye gaze and poor socio-emotional reciprocity, including the hallmark feature of a lack of empathy (Frith, 1989; Frith, 2001). Repetitive and stereotyped behaviours are linked to a lack of imaginative capabilities. However, repetitive behaviours are evident in high-functioning people with autism who are not 'mind-blind' and seem to serve a calming function. Autistic children are less inclined to engage in symbolic play and instead demonstrate a preoccupation with

routine and structure (Turner, 1999). While the current diagnostic criteria reflect consensus on clinical features of autism, there is still no consensus on an explanatory framework that integrates aetiology, neural structures, cognitive processes and behaviour (Happé et al., 2006; Volkmar et al., 2004). However, autism is currently described as a neurodevelopmental disorder with a strong genetic aetiology (Rutter et al., 1997). Since the original accounts of autism by Leo Kanner (1943) and Hans Asperger (1944), several theories of the origin of autism have been proposed. In the following two sections, four (not mutually exclusive) psychological theories proposed to explain the main features of autism will be outlined: the mindblindness theory, the executive function theory, the weak central coherence theory and the recent mirror neuron system (MNS) theory. This last theory, which relates representations of action to TOM impairments in ASD, will be the focus of the experiment in this chapter.

6.2. Psychological theories of autism

6.2.1. The mindblindness theory

The central tenet of the mindblindness theory is that impairment in TOM, or in the ability to 'mind-read', causes an inability to infer the mental states of others or to predict their behaviour, which in turn leads to the hallmark social interaction problems seen in autism (Baron-Cohen, 1995). The False Belief test (cf. Dennett, 1987) designed by Wimmer and Perner (1983) (discussed in Chapter 1), has been central to the development of the mindblindness theory of autism. As described earlier, this test distinguishes between one's own knowledge of reality and the understanding of another person's belief about reality. The first study involved administering the False Belief Test to autistic children, children with Down's Syndrome and typically-developing (TD) children (all matched on verbal and non-verbal ability IQ). The results demonstrated that the children with autism were specifically impaired in TOM (Baron-Cohen et al., 1985). The children with Down's Syndrome passed the false belief task like the typical children, whereas the autistic children did not pass the test. This finding has since been corroborated by several other studies showing that autistic children do not show the same awareness of social elements of other agents' mental lives as do TD children (see Frith, 2001; Hill & Frith, 2003, for reviews).

Children with autism are often impaired on several tasks of first-order TOM that involve inferring someone else's beliefs (Baron-Cohen et al., 1995; Perner et al., 1989; Swettenham, 1996). Ordinarily, children aged four can pass these tests. In addition, unlike TD children aged five to six years, children with autism are often unable to pass second-order TOM tasks that involve inferring what one character thinks about another character's belief (Baron-Cohen, 1989). In addition, unlike TD children of the same age, they are less likely to spontaneously generate mental state words such as 'imagine' or 'wish' in their speech (Baron-Cohen et al., 1986) and have trouble understanding other people's mental states and intentions in speech, shown for example, in their inability to follow sarcasm, irony or metaphors (Happé, 1994). While TD children aged two can distinguish between real acts and pretend acts (Leslie, 1987), children with autism have problems with pretence. They are less likely to engage in pretend play (Baron-Cohen, 1987), which indicates an inability to understand the notion of pretence, most likely because appreciating pretence requires an understanding of the intentions of the actor and the ability to distinguish between reality and belief. Furthermore, while autistic children can comprehend the physical causes of emotions, such as pain causing sadness, they are less able to comprehend mentalistic causes of emotions, such as a particular belief causing sadness (see Baron-Cohen et al., 1993). Like TD children, children with autism are able to understand physical representations, but there appears to be something particular to mental state representations that is impaired in autism (Charman & Baron-Cohen, 1995). Children with autism also have problems decoding social information from faces: while TD children can infer mental states from eye gaze, children with autism are impaired at this (Baron-Cohen et al., 1995).

Together, these studies suggest a specific delay in the development of mindreading in children with autism (Baron-Cohen, 1991b), which might also be apparent from joint attention problems at the early stage of around 20 months of age (Charman et al., 1997). As described in Chapter 1, joint attention indicates an awareness of other people's subjective worlds, and has been proposed to be a precursor to mindreading (Baron-Cohen, 1991). It is thought that a parallel impairment in the normal trajectory of development of brain areas related to TOM and joint attention, such as MPFC, STS and temporal poles, might be causally linked to these mindreading problems in autism (cf. Frith & Happé, 2005; Hill & Frith, 2003). However, the mindreading theory does not explain the tendency of autistic people to show repetitive and perseverative behaviours.

Furthermore, it has been emphasised that a number of individuals with ASD do pass TOM tasks (e.g. Baron-Cohen et al., 1985) and that other clinical groups (such as those with schizophrenia (e.g. Corcoran, 2000)) also show TOM deficits (Tager-Flusberg, 2001). In addition, limitations in semantic and syntactic knowledge have been shown to be associated with TOM performance (Tager-Flusberg, 1996). A mindreading theory as a unitary explanation has been called into question on account of the difficulties in applying TOM impairments either universally, or specifically, to autism (Tager-Flusberg, 2001; Tager-Flusberg & Joseph, 2003).

6.2.2. The executive function theory

It has been suggested that executive deficits may have a causal role in the social communication impairments in autism (Dawson et al., 1998). Executive function refers to the mental operations that enable us to disengage from the immediate context and to coordinate our behaviour in a manner that is flexible, strategic and goal-directed (Shallice, 1988). A frontal lobe based "central executive", or Supervisory Attentional System, is conceptualised to govern these mental operations, which include working memory, planning, selective attention, generativity and inhibition of pre-potent responses (Baddeley, 1991; Shallice, 1988). Patients with PFC damage perform poorly on tasks designed to tap executive function (Shallice, 1988). Similarly, autistic individuals perform significantly worse than controls on these tasks (Hughes et al., 1994; Ozonoff et al., 1991; Russell, 1997). Drawing on these findings, it has been suggested that executive function deficits might explain the impairments in the ability to engage in social interactions. The relatively poor performance in these tasks is thought to reflect an inability to integrate online information and selectively attend to different aspects of the environment that might have social importance (Rumsey & Hamberger, 1988). These findings have also suggested that the brain based origins of the cognitive features of autism may be the frontal lobes (Ozonoff et al., 1992). However, people with autism can pass certain executive function tasks (cf. Baron-Cohen, 1999). Furthermore, executive dysfunction is common to other behavioural disorders such as attention deficit with hyperactivity disorder (ADHD) (Grodzinsky & Diamond, 1992) and schizophrenia (Stirling et al., 2006). The executive function theory, therefore, may not be sufficiently specific to explain the autistic phenotype.

6.2.3. The weak central coherence theory

The weak central coherence (WCC) theory poses that certain characteristics of individuals with autism arise from a failure in the normal propensity to form coherence over several stimuli and to integrate them into a context or "Gestalt" (called "weak central coherence" theory; Frith, 1989). This theory describes the processing style that leads autistic people to perceive complex stimuli in a piecemeal manner, as disparate parts rather than a collective whole. This theory was originally put forward to explain the restricted and repetitive behaviours seen in autism, such as highly circumscribed interests (e.g. underground maps), extreme sensitivity to slight changes in the environment and interests in particular details of toys rather than their whole function (Frith & Happé, 1994). This theory has also been put forward to explain why some people with autism demonstrate remarkable abilities in certain areas, while still demonstrating features of autism such as profound social and language impairments (Happé, 1999).

There are several lines of evidence for WCC theory. It has been argued that superior performance on the Block Design test, a part of the Wechsler intelligence test (Wechsler, 1991), which requires the participant to break down a geometric design into its component parts, is due to the tendency of individuals with autism to see the discrete elements rather than the whole context (Shah & Frith, 1993). This same phenomenon has been shown through other tasks in different domains, including reading and perception of shapes (Happé, 1996; Shah & Frith, 1983). Children with autism fail to take into account information about meaning when pronouncing words which may be alternatively pronounced (e.g. 'tear in her eye' versus 'tear in her dress' (Happé, 1997). In this example, the correct pronunciation of 'tear' depends on understanding the word in the context of the whole phrase, not just on enunciating the letters of the single word. Similarly, on the Embedded Figures Test, which requires participants to identify simple shapes hidden in familiar pictures, participants with autism perform significantly better than those with mental retardation and typical controls, due to their insensitivity to the broader context when processing information (Frith & Happé, 1994). In contrast, in these tasks, control groups without autism tend to show a global style of processing, using information holistically to derive meaning. This theory also explains why individuals with autism can have 'islets of ability' with certain types of task. It is possible that weak central coherence and mindreading impairment theories together are

required to explain social deficits in autism, since some individuals with autism can pass TOM tests but show weak central coherence (Frith & Happé, 1994).

6.3. A mirror neuron system dysfunction theory for autism?

6.3.1. Mirror neuron system malfunction in autism

It has been argued, however, that none of the theories outlined above is sufficient to account for the triad of impairments in autism. For example, while the notion that there is an impairment in the capacity to 'mind-read' explains many of the socio-communicative features in autism, it cannot account for motor problems. Further, it has also been proposed that the problem is one of emotional engagement with others and that a focus on TOM is too narrow (Hobson, 1993). Recently, some researchers have suggested that the neurobiological findings from non-human and human primate studies of a "mirror neuron system" (MNS) might provide a cognitive model that is also neurophysiologically based (e.g. Williams et al., 2001). As described in detail in Chapter 1, mirror neurons are a class of neurons found in monkey ventral premotor cortex, that are activated both by the execution of an action as well as the observation of another agent performing that action (cf. Rizzolatti & Craighero, 2004). In the human brain the MNS comprises inferior frontal gyrus, inferior PFC and STS.

It has been suggested that a failure of proper development of the MN system plays a causal role in the development of autism, since MNs are thought to be a substrate for representations of actions that bridge the self to others. Impairment in the understanding of other people's actions is proposed to lead to a deficit in TOM, which in turn would be manifest from an early stage in a poor quality of self-other interactions such as imitation, joint attention and emotion-sharing (Williams et al., 2001). The implication is that problems with certain types of action may be at the root of the developmental cascade that ultimately leads to social communication problems in autism (Gallese, 2006). It is possible that *imitation*, an action that involves engaging with others, also thought to be a precursor to TOM and potentially related to non-social motor and executive functions, is central to an explanatory account of autism (Williams et al., 2001). Imitation, in turn, is thought to rely on a functioning MNS in the brain, which links representations of what is seen to what is done (Iacoboni et al., 1999).

6.3.2. Imitative deficits arise from mirror neuron system dysfunction

The starting point of the MNS dysfunction model of autism (Ramachandran, 2000; Williams et al., 2001) is that, in normal development, imitation is intimately connected to TOM because it involves "translating from the perspective of another individual to oneself". This is similar to the theory proposed by Meltzoff and Decety (2003), who connect mirror phenomena in humans with TOM, using evidence from developmental psychology and functional neuroimaging to argue that the "neural mirror system begets TOM," via imitation (Meltzoff & Decety, 2003, pp. 491). They review infant studies showing motor imitation of facial gestures in healthy newborn babies (Meltzoff & Moore, 1977), to argue that the coding of perception and generation of actions is innate in humans. Meltzoff and Decety (2003) suggest that action representations of the observed acts unify the self and other. In other words, humans are able to store internal models of motor acts to match their observed action and establish a correspondence between the self and other. The fact that babies can imitate actions has led to the interpretation that the ability to translate behaviour seen in others to behaviour of the self is set in place very early on in human development (Meltzoff & Gopnik, 1993). The second line of argument appeals to simulation theory which proposes that we come to understand other people's mental states by internally imitating, or simulating, other people's actions in our own minds (Gallese, & Goldman, 1998) (see Chapter 1). This ability may be a precursor to the understanding of other people's mental states. Thus, as Williams and colleagues (2001) suggest, a failure to represent another person's actions in one's own brain may have consequences for the development of social and emotional engagement with others.

That an imitative deficit might explain the social deficits in autism was first proposed by Rogers and Pennington (1991). They suggested that a lack of imitative propensity during early childhood may be underpinned by a brain based impairment that could account for the constellation of symptoms in autism. This proposal is corroborated by several consistent findings showing differences in the propensity and style of imitation between groups of participants with and without autism (e.g. Hobson & Lee, 1999; Rogers et al., 1996) and indeed, indicates a problem in mapping action representations of others onto the self in individuals with autism. Impairment in the MNS might also account for the non-social features of autism, such as repetitive and stereotyped behaviour (Williams et al., 2001). Williams and colleagues (2001) propose that as well

as intrinsically social phenomena, malfunctioning of the perception-action linkage system might also underpin imitation-related phenomena that are aberrant in autism, including echolalia, the mimicry of words without the normal links to goals or meaning. It is suggested that the inhibitory component of the MNS, required to prevent the actual execution of actions during internal simulation, is somehow impaired in autism. This leads to inappropriate mimicry, without reference to the meaning of the action and therefore without the normal social significance of imitation. Part of the problem, in other words, might be that meaningful actions are learned by imitation, which is impaired in ASD.

6.3.3. Imitation and the mirror system in the normal brain

Equivalent brain areas are activated in the human brain by execution, observation and imitation of actions and it has been argued that this reflects that a function of this proposed human MNS may indeed be to imitate other people's actions (Arbib, 2002; Iacoboni et al., 1999; Rizzolatti et al., 2002). Using fMRI, Iacoboni and colleagues (1999) have shown that in normal adult participants, the activity in anterior PFC and Broca's area during execution and observation of a finger movement also occurred and was augmented during the imitation condition (Iacoboni et al., 1999). This showed that the MNS is active in the human brain during imitation. However, the human brain is not wired to simply resonate with other people in action. The way the human brain responds to the observation of actions is influenced by the goals of the actions. When asked to hold in mind an action to later imitate, brain activity increases are seen in prefrontal and inferior PFC (Decety et al., 1997; Grèzes et al., 1999). Prefrontal activity is thought to reflect the top-down effect of intention processing (Meltzoff & Decety, 2003) and inferior parietal activity might be involved in maintaining the distinction between agents during actions (Ruby & Decety, 2001). As described in Chapter 2, the experiment by Ruby and Decety investigated brain activation differences and overlaps during imagination of one's own versus another's actions, and showed that inferior parietal activity is associated with action imagery and that activity is lateralised according to who the agent of the action is (Ruby & Decety, 2001). Furthermore, brain activity during imitation is influenced by the visual perspective from which the action is observed (Jackson et al., 2005). Imitating an action from the first person perspective (1PP) is associated faster latencies and fewer errors, compared to the third person perspective (3PP), as well as relatively higher activation in the sensorimotor cortex,

indicating a cognitive advantage for the 1PP. This is thought to be due to the relative ease of mapping 'Like me' actions compared to others' actions, and the imitation in the two perspectives relies on distinct neural mechanisms (Jackson et al., 2005). These findings reflect the notion that intentions, perspectives and agency are also coded in the brain during overt and covert imitation of other people's actions, suggesting a link between imitation and social cognition.

6.3.4. Evidence for dysfunction of the mirror system in the autistic brain

The prediction that follows, therefore, according to the theory that MNS dysfunction gives rise to social impairments in autism, is that the neural substrate of imitation will not show the same pattern or intensity of activity as healthy controls in people with ASD. Indeed, neurophysiological evidence from MEG, EEG, TMS and fMRI has emerged in recent years in support of anomalous perception-action coding in individuals with ASD. For example, the mapping of action observation and execution was shown to be weaker in adults with ASD compared with healthy controls in a study that involved applying TMS over the primary motor cortex during the observation of meaningless finger actions (Théoret et al., 2005). In control participants, action observation selectively enhanced motor output to the muscles involved in the movement. However, in the ASD group, this selective excitation was significantly weaker. In addition, the task involved modulating the perspective of the action in relation to the observing participant, such that it was either towards (allocentric view) or away from (egocentric view) the viewer. In the egocentric condition, muscle facilitation was absent during observation of the action, which was interpreted to reflect a deficit in self-consciousness. Furthermore, an EEG study of high functioning individuals with ASD, spanning a large age range including children and adults, provided results that support the notion of MNS dysfunction in autism (Oberman et al., 2005). Here, *mu* wave suppression was used as an indicator of MN activity during observation of actions. There was a lack of *mu* wave suppression in the ASD group during action observation, while there was suppression in the control group during the same condition. It is possible, however, that the interpretations from these data were obscured by the large age range (6-47 years) included in the small sample size (N(ASD)=11; N(control)=13).

Recently, data from an fMRI study, based on the paradigm involving observation and imitation of finger movements, previously used by Iacoboni and colleagues (1999), has

shown differential patterns of brain activity during action observation and imitation in the right parietal lobe and right TPJ, between adolescents with ASD and TD adolescents, aged approximately 15.5 years (Williams et al., 2006). Both groups showed augmentation of somatosensory cortex activation during imitation conditions, relative to other execution conditions, similar to the finding by Iacoboni and colleagues (1999) in normal participants. However, activity in this area was less extensive in the ASD group during imitation. In the ASD group, this reduced activity in somatosensory cortex was paralleled by diminished activity during non-imitative execution conditions, suggesting the possibility of poorer proprioceptive feedback in ASD. Furthermore, the ASD group demonstrated greater activity in DLPFC during imitation, suggesting that this group was relying on visuomotor learning strategies rather than mirror phenomena. Another interesting finding was the activity at the right TPJ, normally associated with TOM (cf. Saxe et al., 2004), was found during imitation but not observation in the control group, but in the observation and not imitation condition for the ASD group. It was speculated that, normally, TPJ activity during imitation influences perception (thus linking action understanding to social understanding), but that this is absent during imitation in individuals with ASD (Williams et al. 2006).

In line with the notion that MNS dysfunction might be linked with social cognitive deficits in autism, an event-related fMRI study demonstrated that children with ASD showed no MNS activity while imitating and observing emotional expressions of anger, fear, happiness, neutrality and sadness, compared to age and IQ-matched TD children who did show reliable MNS activity during this task (Dapretto et al., 2006). Specifically, during imitation of emotional expressions, the TD children showed activity in areas previously associated with MNS activity in adults including premotor regions, amygdala, cerebellum as well as strong activity bilaterally in the pars opercularis in IFG. In contrast, children in the ASD group showed significantly less activity in anterior regions of the MNS, and most notably, an absence of activity in pars opercularis of IFG. TD children also showed greater limbic activity than ASD children. Intensity of activity in the pars opercularis was also shown to correlate negatively with symptom severity in the ASD group. The authors speculated that these results reflect an impairment in the ASD group in the system enabling emotion understanding via action representation (Dapretto et al., 2006). However, it is unclear whether these differences in brain activity

arise from behavioural differences in performance inside the scanner. In addition, the number of participants was low in this study (N=10).

In summary, certain lines of evidence from developmental psychology and neuroscience studies have led to the theory that action understanding is impaired in ASD. The functional neuroimaging findings described above support the proposal that malfunctioning of action coding neurons in the autistic brain lead to impairments in the self-other representations necessary to transform visual perceptions into actions. At the cognitive level, the ability to represent actions, thought to be crucial for encoding actions and subsequently intentions and emotions of others, is as a result thought to be impaired in autistic syndromes.

6.4. Experiment 5: Action representation in adolescents with ASD

6.4.1. Introduction

Clinical and experimental data demonstrate that autism is associated with motor stereotypies, problems of fine motor control, as well as higher social cognitive deficits (e.g. Baron-Cohen, 1991a; Milne et al., 2006; Smith & Bryson, 1994; Turner et al., 1999). The core characteristics of autism, including difficulties in social interaction and repetitive behaviours, are shared by other diagnoses within the broader category of Pervasive Developmental Delay (PDD) (APA, 2000), all of which are encompassed by the term autistic spectrum disorders (ASD) (National Institute of Mental Health, 2004). While motor development is not considered a criterion for diagnosis, there is much clinical and experimental evidence to suggest differences in gross and fine motor skills as well as overall motor development between TD school-aged children and those with ASD (Berkeley et al., 2001; Manjiviona & Prior, 1995; Mari et al., 2003; Mayes &Calhoun, 2003; Provost et al., 2006).

The MNS dysfunction theory of autism would predict that atypical attributes of action representation might account for both motor and social cognitive problems in ASD (Williams et al., 2001). Given this hypothesis, action representations might be expected to be different in individuals with ASD compared with normal controls. As described in the previous chapter, an action representation (or internal model) is a neural system that simulates the dynamic behaviour of the body in relation to the environment (Wolpert et

al., 1995). An internal model can be thought of as a schema, which is composed of information from one's own cognitive mechanisms as well as from the external world (Neisser, 1976). It has been proposed that these internal models make predictions about actions, limb kinematics and parameters of the external world and enable successful planning and execution of movement (Wolpert, 1997). As well as being important for motor control, as detailed in Chapter 1, it is proposed that these predictions are necessary for making distinctions between the self and other, and therefore, are implicated in social cognition.

As described above, neuroimaging studies point to a difference between autistic and control groups in the functioning of the brain regions thought to be linked to the MNS. However, behavioural paradigms designed to tap action representations are also instructive in this regard. Given that the discovery of the MNS is fairly recent, and the hypothesis for their involvement in autism even more so, very few behavioural studies have specifically investigated action representation in autism and existing results are equivocal. For example, Zalla and colleagues (2006) investigated how the understanding of others' actions relates to the inference of goals and intentions in autism using a picture-sequencing task. The task required three groups of participants - adolescents with autism, adolescents with mental retardation and TD adolescents – to arrange picture sequences depicting different types of goal-oriented activities in the correct order of execution. While all groups were able to recognise the actions, participants with autism took a significantly longer time and made more errors than both control groups when sequencing the object-related actions. Given that the task was hypothesised to require the representation of goals in relation to each action, the authors concluded that the findings reflect a pervasive deficit in representing and performing purposive actions in ASD, which cannot be ascribed to general intellectual deficits (Zalla et al., 2006).

It has been suggested that proposed deficits in action understanding in ASD might have a basis in impaired action representation at the level of forward modelling (Gallese, 2006). A postural anticipation task, in which EMG was used to record latencies of kinematic and muscular events showed that the latencies were significantly longer for voluntary unloading using the forearm in ASD (aged 5.9 to 10.6 years) compared to TD children (aged 4 to 8 years). It was therefore suggested that ASD children are impaired

in generating the internal action representations necessary for the anticipation of postures for a bimanual loading task (Schmitz et al., 2003). On the other hand, a recent study showed that children with ASD performed more poorly than verbal age matched-children TD children on TOM tasks and on a meaningless posture representation task, but that performance was no worse in ASD than TD children on goal-oriented action representation tasks, assessing goal-directed imitation, mirror imitation and graph planning (Hamilton et al., submitted).

Similarly, another recent study of internal models of action showed no difference between ASD and control subjects (Blakemore et al., 2006). A tactile stimulus was applied to the palm of the hand using a mechanical device that was controlled either by the subject (self-produced condition) or by the experimenter (externally produced condition). Like control participants, ASD participants rated the self-produced touch as significantly less tickly and intense than the externally generated touch. This attenuation of self-produced sensory stimulation suggests that their internal models are intact. While the participant numbers are small in this study, the conclusion drawn was that there is no difference in forward models of action between AS and control adults. In contrast, the AS participants gave higher ratings than the control participants for both self-produced and externally generated stimuli. This supports the notion that autism is associated with hypersensitivity to sensory stimulation.

It has been hypothesised that PC and cerebellum are two putative brain substrates for internal models of actions (cf. Blakemore & Sirigu, 2003). Volumetric calculations from MR images and anthropometric measurements of head circumference have suggested that macrocephaly, or enlarged brain volume, co-occurs with autism in a proportion of approximately 20% of cases (Courchesne et al., 2001; Fombonne et al., 1999; Lainhart, 2003). Specifically, reduced or normal brain size at birth is followed by rapid brain growth which then ceases between age two and four years, before the typical age of diagnosis (Redcay & Courchesne, 2005). Redcay and Courchesne (2005) indicate that this early wave of brain growth results in a brain size that is equivalent to the size of the adolescent brain. In MR images, the brain enlargement is reflected by increased cerebral grey and white matter. It is speculated that a lack of synaptic pruning underlies the early brain growth (DiCicco-Bloom et al., 2006; Frith, 2003), and brain areas that have been particularly implicated with abnormal morphological development include

the cerebellum and PFC (e.g. Courchesne et al., 1993; Courchesne, 1991). It is possible therefore that abnormal synaptic pruning in these brain areas may impact upon internal model prediction involved in action control and representation in individuals with ASD.

In the current experiment, internal models were investigated using one of the motor imagery tasks used in the study of action representation in normal adolescence, described in the previous chapter. This task, called the Fingers task, requires participants to perform a simple hand action and to imagine the equivalent action, as fast and as accurately as possible. Reaction time is recorded for both, and the correspondence between Execution (E) and Imagery (I) times is used an index of how well the action is internally represented. This phenomenon is based on previous studies of motor imagery that demonstrate a robust effect of equivalence in timing of actions whether they are performed overtly or covertly (Decety & Jeannerod, 1995; Sirigu et al., 1995; 1996). The motor image is proposed to be a conscious equivalent to an action representation, endowed with identical properties (Jeannerod, 1997). As described in the previous chapter, this correspondence in timing occurs because the same speed and accuracy constraints required to perform an action in reality (Fitts, 1954) are represented in the brain in order to imagine that action (Jeannerod, 1997). Therefore, in order to point to increasingly small targets, actions would slow down in order to maintain accuracy. This relationship between timing and accuracy has been mathematically expressed by Fitts' Law (Fitts, 1954). The same relationship holds true when simply imagining an action, which is manifest in the equal timing for motor execution and imagery, in various types of task performed by healthy adults, from writing to walking (Decety & Jeannerod, 1995; Decety & Michel, 1989). This relationship in timing breaks down in parietal lesion patients (Sirigu et al., 1996). This is in line with functional imaging evidence that this brain region is associated with motor imagery (Lacourse et al., 2005; Stephan et al., 1995).

The experiments in the previous chapter of this thesis showed that TD adolescents are able to represent actions, as indexed by a significant positive correlation between E and I in the results from three different imagery tasks. However, their E-I correlations were significantly lower than those of adults, suggesting that the ability to form accurate motor images is still developing during adolescence. Here, the correlation between E and I in the Fingers task was compared in adolescents with ASD and age and IQ-

matched TD adolescents. To assess the relationship with fine motor skill, performance on the Grooved Pegboard task was additionally compared between groups. This is the first time that motor imagery ability has been investigated in individuals with ASD, and the prediction was that the E-I correlation would be significantly lower than that of the TD controls, perhaps as a result of abnormality in neural networks in PFC and cerebellum, brain regions associated with internal models.

6.4.2. Method

6.4.2.1. Participants

36 male participants were recruited in total. The first group comprised 22 adolescents with ASD (mean age 15.3±0.21 years) and the second group comprised 14 age- and IQ-matched TD adolescents (mean age 15.0±0.67 years). Of all the participants included in the study, three in the ASD group and two in the TD group were left-handed. The dominant hand of the remainder of participants was the right. TD adolescent participants were from state comprehensive primary and secondary schools in the London area and ASD adolescents were drawn from the Special Needs and Autism Project (SNAP), a screened population cohort of children born between July 1, 1990 and December 31, 1991, situated in a circumscribed area of South Thames, UK (Baird et al., 2006). The study was approved by the South East Multicentre Research Ethics Committee, and informed parental consent was obtained for all children recruited for this study. In the TD group, none had a history of psychiatric, neurological, developmental or learning disorder. All children in the ASD group had a consensus clinical diagnosis of ASD from three clinical investigators on the basis of in-depth assessments including the autism diagnostic interview-revised (ADI-R) and the autism diagnostic observation schedule-generic (ADOS-G) (See Baird et al., 2006 for details of recruitment and diagnosis procedures for SNAP cohort). The Wechsler Abbreviated Scale of Intelligence (WASI) was administered to each participant individually to assess IQ. Participant demographics are shown in Table 6-1, demonstrating no significant differences between groups with respect to IQ and age.

6.4.2.2. Experimental procedure

6.4.2.2.1. Pegboard task

The Grooved Pegboard Test consisted of a square board with 25 grooved holes. Participants were required to place grooved pegs into the matching holes. The grooves

required participants to rotate the pegs in order to insert them into the appropriate holes. Participants were instructed to perform the task as quickly as they could. The total time taken to complete the task, that is, to fill all the holes with each hand, was recorded for each participant. The speed is an indicator of simple visuo-motor control and dexterity. Participants were tested once on each hand, starting with the dominant hand.

6.4.2.2.2. Fingers task

During the piloting stage, the order of blocks was counterbalanced between participants, so that some started with the Imagined condition and others with the Executed condition. It was found that starting with the Imagined condition was challenging for subjects, who reported not knowing what to imagine. Therefore, it was decided that, during the actual study, participants would perform the tasks in blocks of Executed actions followed by Imagined actions.

The fingers task was identical to that described by Sirigu et al. (1996), and replicated from the previous adolescent study of action representation, described in Chapter 5 (see Method, Chapter 5 for full details of Executed and Imagined conditions, as well as Instructions). Two blocks of Executed actions were followed by two blocks of Imagined actions, with each block consisting of a sequence of three consecutive, continuous finger actions. The piloting stage with the ASD group indicated that three actions for each block would be more appropriate, compared with five actions as in the previous typical adolescence study.

6.4.2.3. Statistical analysis

6.4.2.3.1. Pegboard task

For each group, the mean time taken to complete the task was recorded for each hand, and overall time, irrespective of the hand used, was calculated. Independent samples t-tests were used to compare mean reaction times between groups.

6.4.2.3.2. Fingers task: individual reaction time data for Imagined and Executed actions

For each participant, the mean movement duration for all the trials (six for each condition) under the Executed and Imagined conditions was calculated. To investigate how well these data correlated across participants, each participant's mean Executed RT

(E) was plotted against his mean Imagined RT (I), for each task. Individual correlations provide information about motor imagery ability, which would be masked by comparing group means. A Pearson's product moment correlation was calculated between the mean E RT and mean I RT.

6.4.2.3.3. Comparison of E-I correlations between groups

Fisher's Z analysis was used to test whether the size of the correlations between executed and imagined movement duration significantly differed between the ASD and TD groups on each task. According to this test, if the Z value was above 1.96, the correlations were significantly different at the $p<0.05$ level, and if the Z value was 2.58 or over, the correlations were significantly different at the $p<0.01$ level.

6.4.2.3.4. The effect of laterality

The effect of laterality for this task was analysed by comparing E-I correlation for the left and right hand within each of the ASD and TD groups.

6.4.3. Results

Data from four ASD participants were excluded as they were unable either to complete or to follow instructions for the Fingers task. IQ and Pegboard task data were not available from four of the TD participants. For the Pegboard task, there were three outliers in the ASD group, whose mean RT fell over 3 SD away from the mean.

Variable	Mean ±SD (ASD; N=18)	Mean ±SD (TD; N=14)	*t*-value	*p*-value
Age	15.3±0.21	15.0±0.67	1.9	.08
Verbal IQ (VIQ)	84.95±11.5	92.8±16.2	-1.5	.14
Performance IQ (PIQ)	95.75±16.8	103.6±18.4	-1.2	.25
Full scale IQ (FSIQ)	89.3±12.8	97.4±17.7	-1.4	.16

Table 6-1. *Participant information. Mean age and IQ scores (including full scale IQ, verbal IQ and performance IQ). As shown by the t- and p-values, there were no significant differences in age or IQ between groups.*

6.4.3.1. Relationship between IQ and tasks

Linear regressions investigating the relationship between IQ and fine motor control as indexed by time taken on the Pegboard task showed that that none of the subscales of IQ have any effect on performance in the ASD group (effect of FSIQ: t=1.1; *d.f.* =3,11; p=.29; PIQ: t=-1.1; *d.f.* =3,11; p=.30, VIQ: t=-1.2; *d.f.* =3,11; p=.24; all N.S.), nor in the TD group (FSIQ: t=-2.1; *d.f.* =3,4; p=.10; PIQ: t=1.6; *d.f.* =3,4; p=.18, VIQ: t=2.6; *d.f.* =3,4; p=.06; all *n.s.*).

The same analyses indicated no effect of IQ on performance on the Fingers task in the ASD group, as indexed by the RT difference, irrespective of direction, between E and I (effect of FSIQ: t=-.62; *d.f.* =3,14; p=.55; PIQ: t=.64; *d.f.* =3,14; p=.53, VIQ: t=.73; *d.f.* =3, 14; p=.48; all N.S.), nor in the TD group (FSIQ: t=.20; *d.f.* =3,4; p=.85; PIQ: t=-.27; *d.f.* =3,4; p=.81, VIQ: t=-.26; *d.f.* =3,4; p=.81; all N.S.). Given that IQ unrelated to any of the dependent variables it was decided to include the four TD participants who did not have IQ data (although parents and teachers had all indicated that the children did not have learning disability).

6.4.3.2. Pegboard task: fine motor control

An independent samples t-test indicated no difference in the time taken to complete the Pegboard task between the ASD group (mean RT±S.E.=85.2±3.7secs) and the control group (mean RT±S.E.=79.7±3.3secs) (t=.959; p=.35).

6.4.3.3. Fingers task: action representation

The correlation between the timing of actual (E) and imagined (I) actions was positive and significant for both age groups (R^2 (ASD)=0.60; R^2 (TD)=0.80; p<0.01 for both). A Fisher's Z test indicated that there was no significant difference in the E-I correlation between groups (Z=1.06; p>.05; *n.s.).* See Figure 6.1.

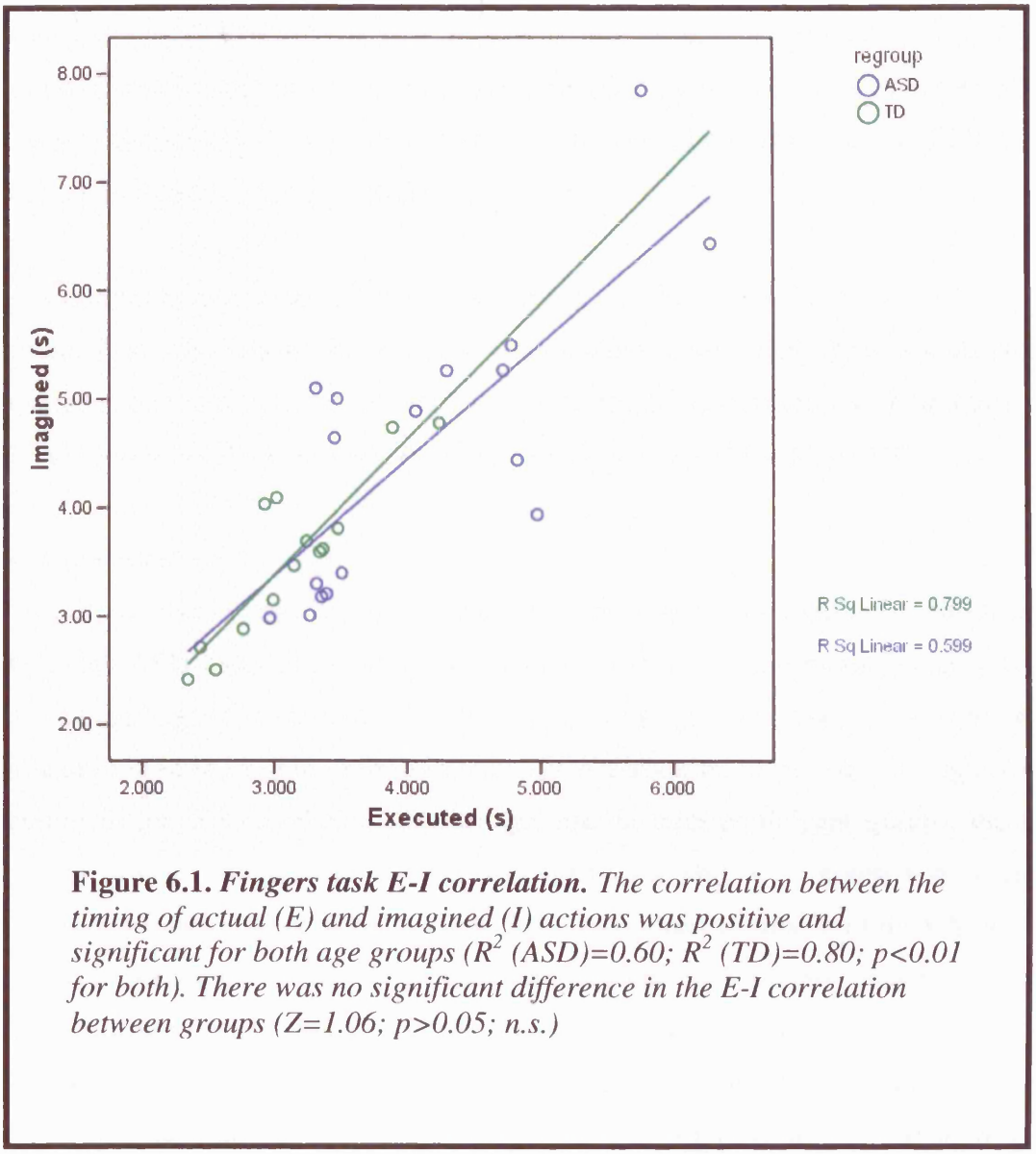

Figure 6.1. ***Fingers task E-I correlation.*** *The correlation between the timing of actual (E) and imagined (I) actions was positive and significant for both age groups (R^2 (ASD)=0.60; R^2 (TD)=0.80; $p<0.01$ for both). There was no significant difference in the E-I correlation between groups ($Z=1.06$; $p>0.05$; n.s.)*

6.4.3.4. Comparison between action times in each group

Independent samples t-tests used to compare the mean E time between groups indicated that ASD adolescents were significantly slower (mean RT±S.E. = 4.10±0.24 ms) than TD adolescents (3.13±0.14 ms) at executing the finger action (t=3.6, $d.f.$=25.6; p<0.005). Similarly, the mean I time of ASD adolescents (mean RT±S.E. = 4.55±0.33 ms) was significantly slower than that of the TD adolescents (mean RT±S.E = 3.53±0.20 ms) (t=2.5, $d.f.$=29; p<0.05).

6.4.3.5. Laterality effects on action representation

As found from the data in the normative adolescent study in the previous chapters, comparisons between E-I correlations for each hand showed no effects of laterality on ability to represent actions (Z (ASD)=0.58, p>0.05; *n.s.*; Z (TD)=.47, p>0.05; *n.s.*).

6.4.4. Discussion

The results of the Pegboard task indicate that there were no significant differences between the ASD and TD group in fine motor control. For the motor imagery task, while the timing of Executed (E) actions as well as Imagined (I) actions was significantly slower in ASD compared to TD adolescents, there was no significant difference in the E-I correlation between groups. In both participant groups, the E-I correlation was significant and positive, suggesting the ability to represent accurately actions is in place in TD adolescents (confirming previous results from the Chapter 5) as well as in adolescents with ASD. This is the first time that a motor imagery task has been used to show that the action representations generated and used for this type of task are in tact in adolescents with ASD. Thus, the data do not indicate that there is a relative impairment among ASD adolescents, in the ability to form motor images. It is worth pursuing this study with a higher N to verify this lack of difference.

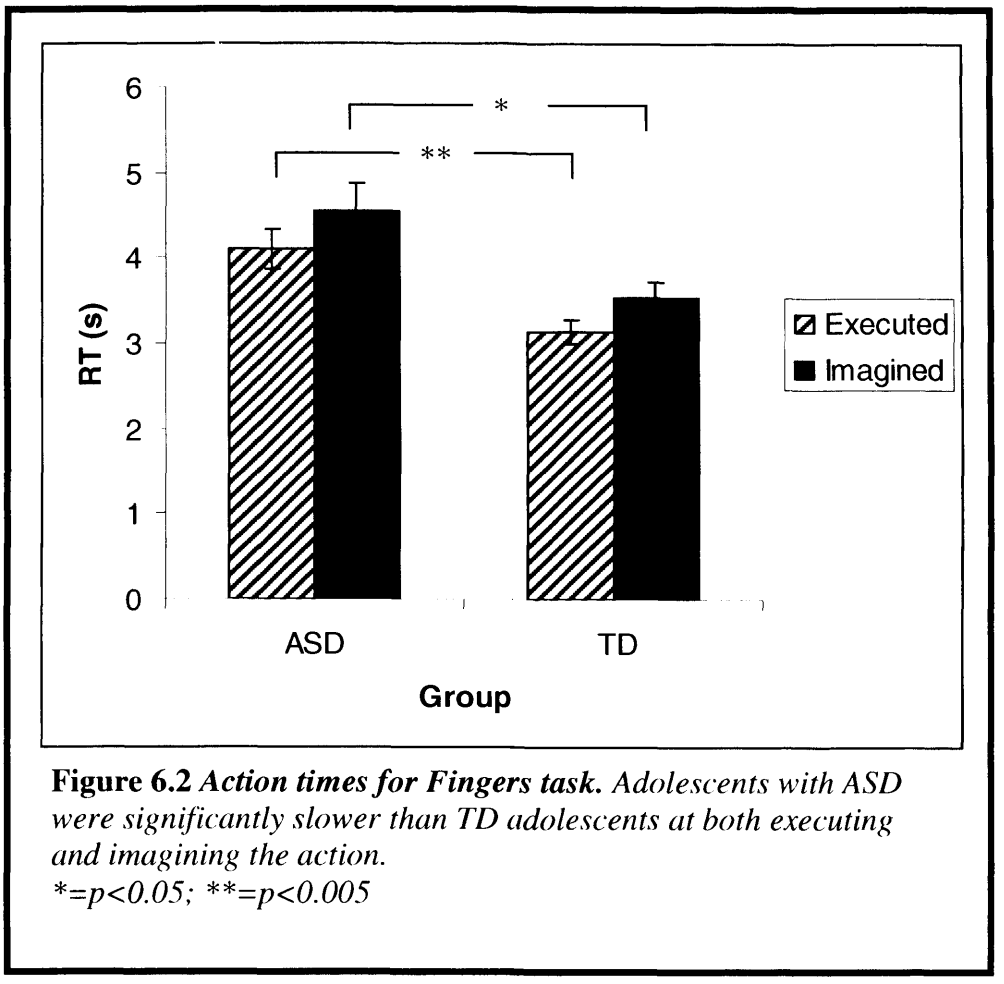

Figure 6.2 ***Action times for Fingers task.*** *Adolescents with ASD were significantly slower than TD adolescents at both executing and imagining the action.*
**=p<0.05; **=p<0.005*

6.4.4.1. Both TD and ASD adolescents are able to generate motor images

The comparison between the mean E time between groups and the mean I time between groups demonstrated that action times in each of the executed and imagery modalities were significantly slower among ASD adolescents than TD adolescents. This may have been due to differences in carrying out the Fingers task, such as generally slower RT among individuals with ASD. However, with respect to the measure of ability to represent actions, the high correlations between E and I in both groups corroborate results from previous psychophysical experiments, supporting the notion that there are parallels between the parameters affecting executed and imagined movements for both adults and adolescents (Decety & Jeannerod, 1995; Decety & Michel, 1989; Sirigu et al., 1995; 1996). In addition, the significant positive E-I correlation for the TD adolescents mirrors the earlier findings from the previous imagery experiments in this thesis, which found, using this Fingers task, as well as two other motor imagery tasks, that adolescents are able to form motor images, as indexed by their high correlation between the timing of E and I actions. The limitation of the current study, however, was that the Praxis Imagery Questionnaire (PIQ) used in the previous normative studies was not used here, due to the time constraints involved in the battery of tasks performed by each ASD adolescent. However, given that there was a tight correspondence between E and I for the ASD adolescents as well as the TD group, it is likely that the Imagery condition was indeed tapping action representation. In other words, ASD adolescents were able to follow the instructions and perform the imagery component of the task properly. It is worth noting, however, that the relatively low N (compared, for example, to that in the normative adolescence study in Chapter 5) might have statistically weakened the E-I correlations in each group. Small sized samples are a general problem in ASD research and might account for the conflicting findings about action representation.

As described in the previous Discussion, this correspondence in timing between E and I reflects the phenomenon that finding from several motor imagery paradigms that subjects make the same speed-accuracy trade-offs for both executed and imagined actions, for example, by slowing down in order to reach accurately to increasingly small targets (Decety & Jeannerod, 1995; Maruff et al., 1999; Sirigu et al., 1995; 1996; Stevens, 2005). The notion that we slow down to ensure accuracy for such actions that we execute has been expressed mathematically by Fitts' Law (Fitts, 1954). Motor

imagery studies with healthy adults have demonstrated that the same relationship holds true for actions that we represent, or imagine (Decety & Jeannerod, 1995; Maruff et al., 1999; Sirigu et al., 1995; 1996; Stevens, 2005). The previous sets of results in this thesis showed that this extends to adolescents and the results reported above indicate that it is also true for adolescents with ASD. In line with the data from the adolescence study in the last chapter, but unlike the study by Maruff et al. (1999), results of the Fingers task indicate that performance is not influenced by laterality for either the ASD or TD adolescent group.

6.4.4.2. No difference in motor imagery or fine motor control between ASD and TD adolescents

Internal models, or representations, of action are thought to be necessary for motor control. As described in the Introduction of Chapter 5, internal forward models are used to maintain accurate motor control by gauging the relationship between predicted states and desired states and providing the motor instructions required by the muscles to accomplish the motor goal, such as the grip force necessary to manipulate a given object (Wolpert et al., 1995). This kind of internal model prediction, which occurs even in the absence of movement (Voss et al., 2006), requires that the relevant information about body kinematics and the relationship to the environment is constantly updated to ensure accurate motor control. Even though the E time for the imagery task was slower among ASD compared to TD adolescence, there was no difference in the timings for the Pegboard task between groups, perhaps because these RTs tap different aspects of motor control. It is possible that the same types of action representations tapped by the Fingers task in the current study are also necessary for the fine motor control required by the Pegboard task. That there were no differences in the performance on the Pegboard task or Fingers imagery task between ASD and TD adolescents suggests that internal models underlying fine motor control are not impaired in ASD adolescents. The implication might be that problems of fine motor control associated with autism are not rooted in internal models of action. While further brain imaging studies are required to test this hypothesis, perhaps the potential effect of parietal and cerebellar tissue abnormalities on the cognitive bases of action, which can occur early in the first few years of life in ASD, are not detected by adolescence. Altered developmental trajectories of brain development that occur following early childhood may for example

be corrective. It is not presently known whether, or how, brain development in ASD during late childhood and adolescence deviates from the normal trajectory.

6.4.4.3. No global action representation impairment in ASD

The results from the current study are in line with a previous study of internal forward models of action in ASD and typical adult controls, which showed no differences in self-monitoring during tactile stimulation between groups (Blakemore et al., 2006). However, the results are at odds with another study described in the Introduction of this chapter, on representation of goal-oriented actions in ASD and typical adults (Zalla et al., 2006). It is possible that action representation is normal in ASD, when tapped by motor tasks *per se*, such as the tickling task or the Pegboard task. However, if the task is loaded by a social cognitive element, such as an intention or social context, representations of actions *are* affected in ASD. In the picture sequencing task of Zalla and colleagues (2006), participants were required to demonstrate action understanding that was linked to making inferences of motives, goals and intentions. While participants with ASD were no worse than controls at action recognition or object identification, their performance was significantly poorer than controls for prediction of purposive actions. These pictures depicted a hand-drawn character performing actions involving objects, where the understanding of the character's intention, in relation to the object and its function, was crucial to predicting the sequential actions. Results from the other conditions in the task also demonstrated an advantage for prediction of physical events compared with person-to-person events, suggesting that the impairment in action representation was restricted to the goal-directed domain.

Even though the task that Zalla and colleagues used did not require the attribution of mental states, there is clearly a higher, social component to the action representations that is required to perform well, unlike those that are tapped in the current motor imagery study, which require the internal modelling of only physical parameters involved in the action and do not involve imaging another person. An earlier study by Baron-Cohen et al. (1986) demonstrated that children with autism performed poorly, compared to control children, on a TOM task but not on tasks involving arrangement of behavioural sequences that represented everyday routine or person-to-person interactions. An interesting line of investigation to follow from the current study would be to determine at what point of 'social loading', action representations become

impaired in ASD, since MN studies suggest their dysfunction. The results of the current study suggest that basic motor representations relevant to simple motor tasks are intact in ASD. These motor simulations are not intrinsically social. The study by Zalla and colleagues (2006) suggest that as the actions become more purposive and involve another agent, action prediction becomes impaired in ASD. Could it be only at the point of representing an action involving another agent, from a third-person perspective that the system breaks down? This would explain why ASD participants fail at TOM tasks and are impaired in joint attention skills but why their forward models of actions seem intact. Data collection is currently in progress to compare performance on a simple mentalising task and on the current motor imagery task in the same ASD and TD adolescent participant groups, to examine the possible links between action representation and TOM in ASD.

The hypothesis that action representation becomes impaired in ASD when loaded with social stimuli fits with the recently proposed theory that autism is a disorder of "intentional attunement" (Gallese, 2006). On the basis of MN studies in the normal population and the few that have been conducted with autistic individuals, Gallese predicts that a disruption to the ability to represent a "we-centric space", by simulating actions and intentions of others, prevents the development of intentional attunement to other agents, which is reflected in the social communication problems in autism (Gallese, 2006). This also fits with the notion that autism is explained by problems in emotional engagement with other people (Hobson, 2002). Gallese suggests that interpersonal engagement problems in ASD may have their origin in action representations such as those used for anticipatory motor control (Schmitz et al., 2003).

Schmitz and colleagues made EMG recordings during a bimanual loading task which required ASD (N=8; age 5.9 to 10.6 years) and TD children (N=16; age 4 to 8 years) to lift a load using the arm. The longer latencies among ASD participants during voluntary unloading were taken to reflect an impairment in the generation and use of action representations required to model the constraints, related to the body and the object, for the action, and this was speculated to be due to cellular abnormalities in the cerebellum. One possible problem that may account for their different finding was the age range. Their assumption was that internal representation for postural control is developed by age 8 (cf. Schmitz et al., 2003, pp. 19). However, the results of the study presented in

Chapter 5 of this thesis suggest otherwise; that action representation continues to be refined during adolescence. Thus, the range of ages used by Schmitz and colleagues may have been a confounding factor. On the other hand, as outlined earlier, a recent finding that ASD children, relative to TD children, were impaired in posture representation as well as TOM tasks, while they were not impaired relative to controls in goal directed imitation, mirror imitation and grasp planning (Hamilton et al., submitted). The authors suggested that ASD individuals might have a problem in representing actions to do with meaningless body postures as well as TOM. The dissociation between TOM and imitation in the study by Hamilton and colleagues suggests that TOM deficits in ASD cannot be accounted for by a single factor explanation of an action representation or MN deficit theory. The implication of the current findings, in the context of previous data, is that action understanding is not a unitary cognitive component, and that different types of action representation may either be impaired or preserved in ASD.It has been emphasised that it is unlikely that any one currently available account can explain all of the behavioural features of ASD. Indeed, it is suggested that ASD is best considered as a multi-system disorder, for which there may not be one unitary explanatory account (cf. Charman, 2006; Happé et al., 2006). Equivocal findings from recent studies, therefore, suggest that it is unlikely that a theory of impairment in action representation, can alone account for the autistic phenotype.

6.4.5. Conclusion

The results in this chapter do not suggest a significant difference between adolescents with ASD and TD adolescents in the ability to represent actions. In line with the findings from Chapter 5, the significant and positive E-I correlation in TD group indicates that the TD adolescents were able to accurately represent actions. The significant and positive E-I correlation in the ASD group was also indicative of this ability and was not statistically different from that of the TD group. This does not suggest an impairment in the action representation system in ASD adolescents, although the sample is smaller than that of the study from Chapter 5. While Gallese (2006) suggests that the problems in motor equivalence between self and other in ASD might be manifest in simple motor control strategies, the data presented here indicate otherwise: low level action representation in ASD is not adversely affected in the type of representation generated and accessed for motor imagery tasks.

7. DISCUSSION

7.1. Studying the development of social cognition from a neuroscience perspective

In the last ten years, the study of the neural bases of social functioning has become a burgeoning enterprise, tying together questions from the social sciences with methods from the cognitive sciences. Most of this work, however, has related to adult or clinical populations. The finding that the human brain develops beyond childhood is relatively recent, while the centrality of social interaction to typical adolescence has long been described. This thesis began by reviewing recent histological and MRI data, which indicate that the normal brain continues to develop during adolescence and into early adulthood. This structural change involves considerable development in the areas of the brain associated with social cognition, including MPFC, STS and PC. Behavioural and fMRI studies have demonstrated parallel development in cognitive processes. Most have focused on executive function and have shown development of inhibition, selective attention, planning and working memory, all thought to correlate with maturation of the PFC (see Blakemore & Choudhury, 2006a,b; Toga et al., 2006 for reviews).

Social cognitive development during adolescence, however, is relatively understudied. Adolescence is considered to be a transitional phase involving changes that extend beyond purely physical development. The Western concept of adolescence is characterised by an emphasis on social behavioural development (Coleman & Hendry, 1990). The purpose of this thesis was to explore empirically the role of developing neurocognitive processes that may contribute to such social behavioural changes. Until now, these questions have been pursued within the realms of social psychology and the social sciences using self-report and interview methods. However, our own notion of 'self' is thought to be constructed through social processes (Mead, 1934), that is through others, and thus the method of studying social cognition that relies on self-reports can obscure processes linking self and other. In addition, in light of the recent data on brain development across the lifespan, neural maturation is increasingly recognised as playing an important role in cognitive development. In the last decade, the emergence of social cognitive neuroscience has provided both conceptual and technical tools to investigate social cognitive development. These tools rely on objective recordings such as reaction

time measures in behavioural tasks and BOLD signals in fMRI paradigms and therefore do not depend solely on subjective reports (Lieberman, 2005).

The experiments in this thesis were designed to explore questions that relate the brain and cognition, and given the developmental context, to be amenable to children and adolescents. These experiments have employed both behavioural and neuroimaging methods suited to children, adolescents and adults. The first task, designed to tap perspective taking, was a novel laptop-based behavioural paradigm that presented verbal vignettes depicting everyday scenarios familiar to all age groups. This was a reaction time task that was designed to be amenable to testing children aged eight and upwards, in schools, as well as clinical patients in a psychiatric unit. Reaction times were taken as an index of cognitive efficiency to carry out the perspective taking task. Previous perspective taking tasks have activated MPFC, IPL and STS in adults (Ruby & Decety, 2001; 2003; 2004).

The second task, which was similarly a novel computer-based verbal question-and-answer task tapping intention understanding, was administered inside the fMRI scanner. fMRI provides an unobtrusive and non-invasive measurement of social cognitive processing. In this study, fMRI proved to be well-suited to testing young adolescents (aged 11 and upwards). This method provided direct evidence of brain function during the intention understanding task and therefore allowed tighter interpretations of brain-cognition correlations.

The third group of tasks (two replicated, one novel) that investigated action representation were behavioural action tasks that relied on a robust cognitive phenomenon based on reaction times for actual and imagined actions. These were simple enough to perform for all age groups tested including a group of adolescents with ASD. The correspondence between executed and imagined reaction times, known to be revealing about the action representation system (Jeannerod, 1997), was the measure of interest.

In summary, all paradigms used for these experiments with children, adolescents and adults, and participants with psychiatric and developmental disorders, were intended to tap social cognitive processes and were designed to do so based on well-replicated

phenomena. A summary of the findings from this thesis is outlined below. These culminate in a possible theoretical model of social cognitive development during adolescence that could be used as a springboard for future research in this field. Limitations of any assumptions involved are also described. Finally, possible applications of these empirical findings to educational and social policy are briefly discussed.

7.2. Developing a shared representation of the world with others

What can be learned from the findings of these experiments about the development of perspective taking, intention understanding and action representation during adolescence? Furthermore, how do the findings relate to the study of social cognition in psychopathology? The combination of behavioural and neuroimaging experiments in this thesis have attempted to track the development of the cognitive mechanisms that underlie the ability to build and share representations of the world with other people. The starting premise is that we must be able to successfully generate our own representations of the world. These then have to be aligned to those of other people in order to understand their perspective on the world and to identify with their subjectivity. One idea that has previously been proposed is that prediction of actions, through internal forward models, might be part of this alignment process. Understanding how these social and motor cognitive processes develop in the typical population allows us to study their possible linkages and also to delineate those mechanisms which go awry in individuals with psychopathological development.

7.3. Developing an understanding of other people's perspective during adolescence

The phenomenon central to these studies is *awareness of others*. The results of Chapter 2, which investigated development of perspective taking in typically developing (TD) adolescents, indicate a development in the efficiency and strategy of perspective taking. Here, the difference in RT between taking the 3PP and 1PP (Δ RT) was used as a measure of proficiency of perspective taking. This difference was pronounced in the pre-adolescents, lower among adolescents and diminished by adulthood. The diminishment of Δ RT with age suggests that there is a refinement in the cognitive mechanism for perspective taking during adolescence. Speculations can also be made

about the link to brain development. Given that previous fMRI studies have shown that simulating how other people act, think or feel activates superior FC and right IPC (Ruby & Decety, 2001; 2003; 2004), the current data were interpreted to reflect a refinement during adolescence in the frontal and parietal based neural networks that support perspective taking. In light of earlier histological data (Huttenlocher, 1979; Yakovlev & Lecours, 1967), these refinements may be considered in terms of development in interconnectivity between networks, through, for example, synaptic pruning and/or axonal myelination.

What remains to be clarified, however, is the nature of this development of perspective taking during adolescence, in terms of its *content*. The findings from Chapter 2 suggest that efficiency in this ability improves. In addition, the scatterplot (Figure 2.4) of RT versus age indicating directionality (3PP>1PP or 1PP>3PP) suggests a strategic shift with age, such that pre-adolescents demonstrate a less systematic style of processing with RTs distributed approximately equally on either side of the zero line (where 3PP=1PP). In other words, half of the pre-adolescents in this experiment took longer to take the 3PP than the 1PP and the other half took longer to take the 1PP than the 3PP. As age increased, the distribution of Δ RTs clustered closer together until adulthood, during which age the distribution was largely along the zero line. The results of this study show that both the magnitude of the difference between 1PP and 3PP (Δ RT) and perhaps also the strategy develop with age during adolescence. A negligible difference in RT between 1PP and 3PP is proposed to be the normative healthy adult response, signifying fast, intuitive perspective taking that depends on mature, fine-tuned and efficient neural networks. Whether a longer RT for one perspective condition, compared to another (e.g. 3PP>1PP), signifies relative *difficulty* in stepping into another person's 'mental shoes' cannot be answered here. If first-person perspective taking takes longer than third-person perspective taking (1PP>3PP), this might suggest an impairment in self-consciousness. Alternatively, taking longer for 3PP versus 1PP may suggest that the participant *is engaging* in third-person perspective taking and able to see the world from someone else's view (but that this process is more effortful and therefore takes longer), while a low RT for 1PP might suggest inability to access one's own point of view (see Limitations and Future Studies).

7.4. Understanding one's own and other people's perspectives in delusional schizophrenia

The results of the perspective taking experiment in healthy adults and adult patients with affective disorders and schizophrenia indicated that affective patients have a significantly higher Δ RT than normal controls, particularly in the Closed condition (Chapter 2). This was contrary to the prediction that schizophrenic patients (those with the highest levels of persecutory delusions) would show the highest Δ RT. On further examination of the data, there was a suggestion that the pattern of directionality of RT-C (3PP>1PP / 1PP>3PP) differed between groups. In the normal controls, there was no difference between 3PP and 1PP (3PP=1PP). In the affective group, most patients showed a difference in the direction of 1PP>3PP and in the schizophrenic group, almost all showed a difference in the direction of 1PP>3PP. However, the relatively low N in both groups must be considered here. This pattern was not shown to be significantly different between groups, most likely because of the small number of patients in the schizophrenic group (N=6). If longer RTs signify relative difficulty, then one interpretation is that affective patients have difficulty in taking someone else's perspective while schizophrenic patients have a problem in self-consciousness. The opposite would be true if longer RTs reflect engagement in the task and shorter RTs a failure to engage in one particular perspective condition.

7.5. Imaginary audiences: present in the population on a continuum?

Does the experience of having an exaggerated awareness of others have a particular profile of Δ RT for the perspective taking task? The data presented in Chapters 2 and 3 provide a starting point for further research into the content of the processing styles in psychiatric patients and TD adolescents. The TD pre-adolescents and adolescents and the affective patients demonstrated Δ RTs in a similar millisecond range. This might suggest something similar in the efficiency of the cognitive systems for perspective taking for these groups (see Figure 7.1). In terms of directionality, the style of pre-adolescents and adolescents is comparable to that of patients with affective disorder and schizophrenia, who showed Δ RTs in both the 3PP>1PP and 1PP>3PP directions. An interesting question is whether there could be something qualitatively similar about the underdevelopment of social cognitive mechanisms in adolescents, and the abnormality

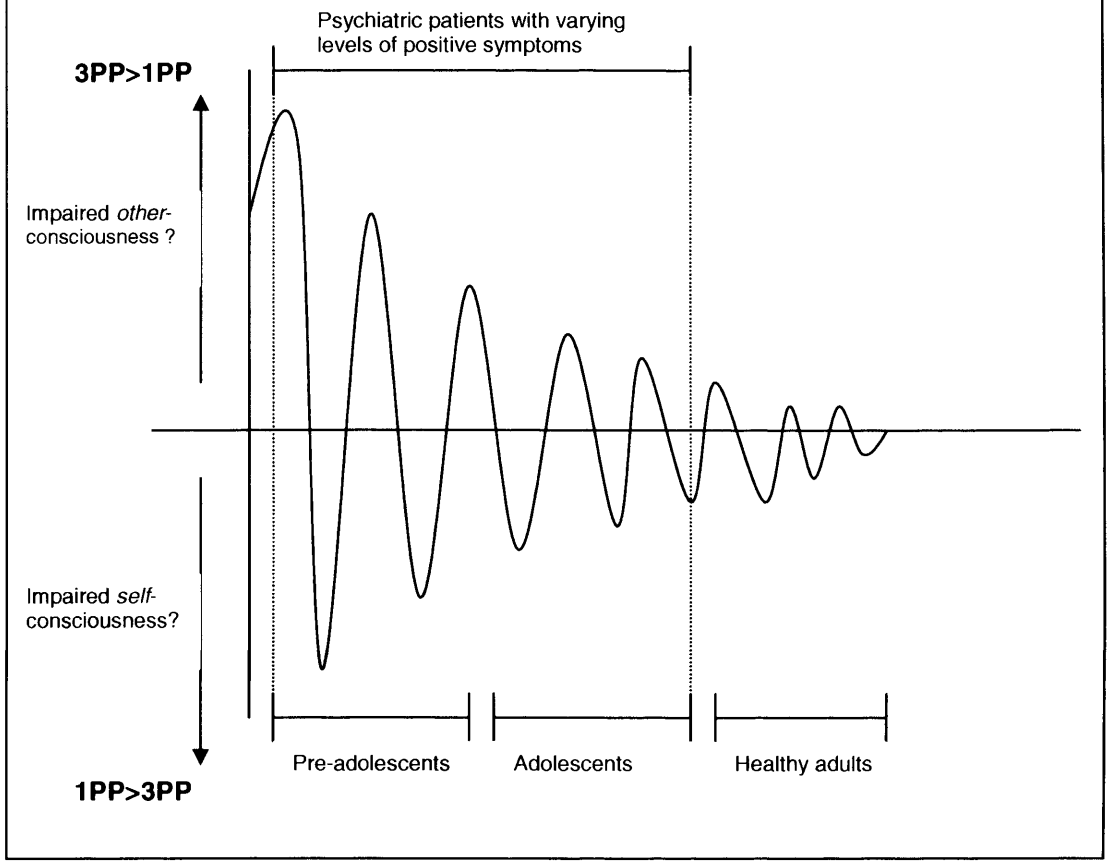

Figure 7.1. ***Imaginary audiences***. *The lack of systematicity in processing emotional perspectives in TD adolescents (Chapter 2) may bear a similarity to that of the psychiatric patients (Chapter 3). This leads to the question of whether there are any qualitative similarities in cognitive processing for altered awareness of the self or others among both healthy and clinical populations.*

of these mechanisms in depressive or delusional states, that is linked to having less alignment between one's own representations of the world and those of others. This may be in the form of exaggerated awareness of other people or impaired self-consciousness. The data presented in this thesis cannot answer this question but may suggest an avenue to pursue.

The notion of the 'imaginary audience' was discussed in the Introduction. This is a construct introduced by post-Piagetian psychologist, David Elkind, to describe the exaggerated awareness of other people's thoughts during typical adolescence (Elkind, 1967). This preoccupation with others tends to be directed towards the self. People with delusions of persecution also have an exaggerated awareness of other people (Bell et al., 2006). These often involve the ascription of malevolent intentions to other people, directed to the self (Frith, 1992). Delusions of persecution exist in the normal population, and are also characteristic, in an extreme form, of some clinical patients with a diagnosis of schizophrenia (Bell et al., 2006).

Some researchers have suggested that delusions are not categorical phenomena that are linked to psychopathology and absent from the normal population, but rather that they exist on a continuum on which they are absent on one end but extreme on the other. This idea is drawn from questionnaire data that show that 10% of the normal undiagnosed population score higher than the mean of psychotic inpatients on delusional ideation measures (Peters et al., 1999; 2004). These data indicate that the form of delusions is not qualitatively distinct from normal beliefs, but that they may represent an extreme version of the anomalous mental phenomena that are relatively common in the typical population.

In a similar vein, some researchers have suggested that the presence of auditory hallucinations may not necessarily signify pathology. Given that the form of these hallucinations is not starkly different in undiagnosed people in the general population who hear alien voices from those that are diagnosed as schizophrenic (Leudar et al., 1997), it has been suggested that auditory hallucinations, too, exist on a continuum of thought patterns (cf. Jones & Fernyhough, *in press*). The finding that subvocalizations could be picked up by a throat microphone from hallucinating patients (Gould, 1949), and that hallucinations could be stopped if hallucinating patients opened their mouths

wide enough to stop the vocalizations (Bick & Kinsbourne, 1987) led to the proposal that inner speech is causally linked to auditory hallucinations. On the basis that inner speech is the 'substance' of auditory hallucinations, Jones and Fernyhough (*in press*) have proposed an explanatory model, which is a variant of Frith and colleagues' model of self-monitoring (Blakemore et al., 2003b; Frith et al., 2000). The authors hypothesise that a failure to predict the consequence of an action, due to the absence of efference copy, leads to a lack of awareness of self-generated inner speech. The subsequent mismatch between the predicted and actual state leads to the experience of external authorship of inner speech (Jones & Fernyhough, *in press*). The authors claim that, according to their framework, "inner speech constitutes a form of verbal self-regulation that is derived from semiotically mediated exchanges with interlocutors in the social world". Thought is therefore essentially social; inner speech retains the dialogic qualities of conversation and thus "thinking is naturally permeated by other voices" (Jones & Fernyhough, *in press*, pp. 6). This theory indicates that verbal speech and inner speech are related, which in turn suggests that inner speech involves similar corrections and adjustments to spoken words.

In keeping with the notion that inner thought is derived from social dialogues, positive symptoms of schizophrenia such as delusions of persecution or auditory hallucinations might be conceptualised, phenomenologically, as an extreme form of the adolescent imaginary audience. Indeed, the mental construct of the imaginary audience is not restricted to adolescents, but has been shown to exist for adults (Vartanian, 2000). However, the degree to which adults and adolescents act on, respond to, or acknowledge the voices or actions of their imaginary audiences clearly differs. Whether or not there is a process of cognitive maturation that enables the inhibition of this manner of thinking, or that social expectations and norms contribute to this development, remains to be investigated. However, the data presented provide a springboard to investigate, in a developmental context, the notion that delusional thinking, or 'imaginary audiences', exist on a continuum. Different developmental trajectories between TD and clinical groups must be taken into account, but it could be worth exploring the possibility that the imaginary audience may be qualitatively similar in adolescents, adults in the typical population who experience magical thinking, persecutory thoughts or who hear alien voices and people with a diagnosis of affective disorders or schizophrenia and who have positive symptoms (see Figure 7.1). Perhaps

these altered states of self/other processing at the higher social level are linked to the ability to read intentions.

7.6. Understanding intentions: a shift in social cognitive strategies with age

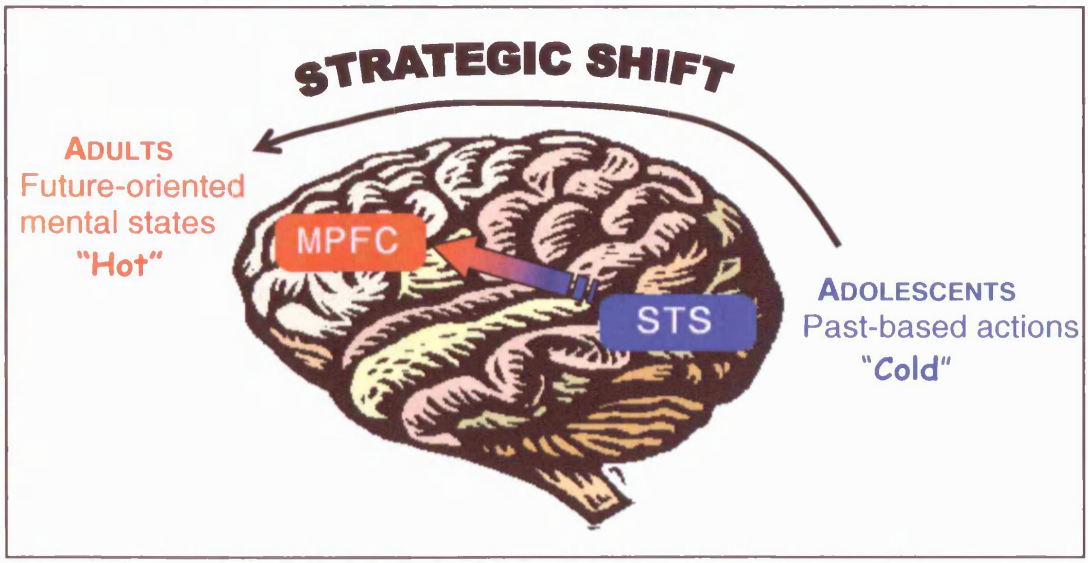

Figure 7.2. ***Strategic shifts in social cognitive processing during adolescence****: It is possible that the shifting neural strategy from relatively higher STS activity to higher MPFC activity for intention understanding (Chapter 4) with increasing age reflects a change in the type of representation generated to achieve the same social goal. To make sense of and predict one's own or others' behaviour, adolescents may represent past actions while adults may be more likely to represent future-oriented mental states.*

The results of the fMRI study described in Chapter 4 demonstrate that there is a change in the pattern of brain activity during adolescence for understanding the consequences of one's own intentions. Specifically, the data indicate a shift with age in recruitment within the mentalising network in the brain, from relatively higher posterior (STS) activation to relatively higher frontal (MPFC) activation from early adolescence to adulthood. Thus, it seems that during adolescence, the neural strategy for thinking about intentional causality changes with age. The posterior-anterior shift might in turn reflect a changing cognitive strategy. The nature of a cognitive strategy shift is suggested by the change in relative roles of brain areas from predominantly STS (associated with actions) in young adolescence to predominantly MPFC (associated with TOM) in adulthood. In order to predict the consequences of an intention, it is proposed that adolescents generate an action based representation that relies on existing motor schema

from past actions ("What would I do?", based on a prediction of an action), whereas adults generate anticipated mental state representations ("What would I do, given how I would feel?" based on one's own imagined mental states). Adults might also base their predictions of intentional actions on representations of *other people's* mental states ("What would I do, given how they would feel?" based on the imagined mental states of others). Thus, increasing MPFC activity with age might suggest the increased incorporation of other people's mental states into self-related computations (Figure 7.2).

Based on the notion that action representation is an early precursor to full blown mentalising, these data indicate a strategic maturation: during adolescence, there is a shift towards a more sophisticated form of intention understanding. Aichhorn and colleagues' suggest that posterior STS/TPJ region is involved in realising that minds represent the world differently and storing "cold" facts about the mind while on the other hand MPFC is thought to represent "hot" information such as predicting the emotional consequences of behaviour (Aichhorn et al., 2006). In this context, the current data reflect a shift in processing style from "cold" to "hot", during adolescence (see Figure 7.2). Again, it might be speculated that this is facilitated by the development of these brain areas and the reorganisation of their interconnections. It is possible that the development of intention understanding has a basis in the way the brain generates representations of action.

7.7. What does the development of action representation tell us about social cognitive development during adolescence?

The experiments described in Chapter 5 using three different motor imagery tasks demonstrated that the ability to imagine accurately an action develops during adolescence. This type of imagery is analogous to unconscious action representation, which is proposed to be necessary for controlling our own actions (Jeannerod, 1997). Action representations are also necessary to predict the actions of others and it is thought that we use this to detect errors in order to refine our representations of mental states of other people with whom we interact. Since the discovery of mirror neurons (MNs) in the last decade, motor theories for self-other interaction have flourished. The central tenet is that we are implicitly bridged to other people through action. More specifically, it is proposed that we are able to read other people's intentions and desires

from their actions because we can map their actions to our own action schema, or representations, and thus make mental state inferences. This idea arose from several variations of the experiments by Rizzolatti and colleagues, which demonstrated that the visual perception of another's goal-directed action elicits a representation of that action in the observer's own brain in both non-human and human primates (cf. Rizzolatti & Craighero, 2004).

While the first perspective taking study showed that the ability to imagine how oneself or someone else feels develops in adolescence, the series of action representation studies showed that the ability to imagine making an action is also refined during adolescence. As mentioned earlier, internal models of actions are thought to be necessary in the understanding of another's intentions (Blakemore & Decety, 2001). A motor image is thought to be a conscious equivalent of efference copy, an integral aspect of the forward model. Efference copy is an exact copy of the motor command. A representation of action, accessed by imagining an action, is therefore analogous to an action prediction. This action prediction is necessary to monitor errors and to make corrections in order to accurately control our actions. The forward model can thus be applied to imagined actions as well as executed actions, since imagined actions are endowed with the same properties as real action plans and are governed by the same parameters (Decety & Jeannerod, 1995).

Could the refinement in action representation and perspective taking during adolescence reflect an association between these two cognitive capacities? It might be speculated that there is in fact a causal link such that the development in the ability to represent actions reflects its necessity for the ability to represent mental states. There are at least two conceptual assumptions made here: firstly, that representing one's own actions is necessarily linked to representing other people's actions, and secondly, that representing another's actions is linked to representing another's mental state. The data described in the Introduction suggest these linkages. Whether or not these two cognitive capacities directly overlap cannot be ascertained from the experiments described in this thesis, since the populations of participants were separate for the two types (perspective taking and motor imagery) of task. The direction of causality, that is, whether action representation is necessary for higher social cognitive processes or vice versa, cannot be determined either. One previously suggested possibility is that action representation is

an ontogenic precursor to mental state representation (Gallese, 2006). On the other hand, perhaps understanding other people's minds guides our subsequent actions and behaviour, such that we act in a way that is aligned with what we predict to be other people's expectations. Either way, that these two abilities continue to develop, if subtly, during adolescence is suggestive of some development during this period of the awareness and incorporation of other people's actions and mental states into one's own cognitive schema.

7.8. Testing the hypothesis that action understanding is impaired in autism

A *lack of* social awareness of others is central to the behavioural phenotype of autism spectrum disorders (ASD). In the final experimental chapter (Chapter 6), the results showed no difference in the ability to represent actions between adolescents with ASD and TD adolescents. It might have been predicted, based on the assumption that action representation is necessary for mental state representation, that the ability to imagine actions would be impaired in ASD. In addition, the role of PCC for action representation, as demonstrated by adult lesion patients, coupled with atypical parietal morphology in the ASD brain might lead to the hypothesis that motor imagery is impaired in ASD. The data presented in Chapter 6, however did not demonstrate this. The correlation between timing of executed and imagined actions, the index of proficiency at representing actions, was lower among ASD adolescents than TD adolescents, but this was not significant. This difference may have become significantly pronounced with a greater N, and data is still being collected to ascertain this. However, the conclusion drawn from the current findings is that the ability to generate action representations is comparable in ASD and TD adolescents.

It has previously been suggested that ASD can be explained in terms of a failure in intentional attunement, that is, the lack of embodied engagement with other people (Gallese, 2006). According to Gallese, this entails simulating the actions, intentions and mental states of other people. Gallese suggests that a deficit in mentalising in ASD is due to an inability to simulate other people's intentions and mental states, which in turn has a root in an impairment in the ability to represent actions. In line with a previous finding from a self-tickling paradigm demonstrating that forward models are not atypical in autism (Blakemore et al., 2006), the current data show no impairment in the

action representations tapped by the motor imagery paradigm. These results suggest that action representations generated for motor tasks *per se*, are not affected in autism. In other words, individuals with ASD are able to represent the physical parameters required to form accurate action representations. It is possible that the impairment in action representation in ASD suggested by Gallese and others is only noticeable when the action task is imbued with a social context, such as a character or an overt social goal (Zalla et al., 2006). However, Gallese's theory about impairments in action simulation in ASD makes reference to one study (Schmitz et al., 2003) that suggests that even anticipatory models of action, that involve posture correction, and thus have no obvious social context, are adversely affected in ASD. Similarly, it has been proposed that there is an imitative deficit in ASD, reflecting impairment in action representation (Dapretto et al., 2006; Williams et al., 2001). This is at odds with the finding in Chapter 6. However, in line with the current results, it has recently been found in that, while children with ASD performed more poorly than TD children on TOM tasks and on a meaningless posture representation task, performance on goal-oriented action representation tasks was no worse in the ASD group (Hamilton et al., submitted). Taken together, it may be argued that there is no global deficit in action representation in ASD, but rather that action understanding is best understood in terms of multiple action systems, some of which are preserved in ASD. Further experiments that replicate action representation tasks, that have larger numbers of participants and have equivalent inclusion and grouping criteria are necessary to investigate the level at which action understanding might be problematic in ASD.

Furthermore, the relationship between action representation and cognitive features of ASD, such as problems with mentalising and repetitive behaviours, require systematic testing. It is unlikely that one account, such as a theory of impairment of the MNS or of action understanding alone, can account for the triad of impairments seen in ASD (Charman, 2006; Happé et al., 2006). Rather, ASD is better viewed as a multi-system disorder, in which action representation might have a connection to one or more of the behavioural features of ASD.

7.9. Dialectics of development: a shift in social cognitive strategies during adolescence

The results of the empirical studies presented here are best interpreted in a framework that views adolescent cognitive development as a process of both strategic shifts and an improvement in ability. Put differently, all of the experimental studies presented here showed that both adults *and* adolescents were able to perform the tasks. Thus, it is not as if adolescents are impaired in social cognition. Indeed, it is well established that four year-old children have a TOM (Wimmer & Perner, 1983). What is apparent, however, is a subtle refinement in *the way* in which the tasks are performed. The notion of this kind of dialectical development in relation to adolescent cognitive development is apparent in the writings of Piaget on stages of cognitive growth. The suggestion is that there is a transformation, or a development in the *form*. A distinction is therefore made between the *level* (degree of ability) of processing and the *form* (strategy) of processing (see Figure 7.2).

As described in the Introduction, the development of egocentrism from childhood through adolescence has previously been described in dialectical terms (Elkind, 1967), that is, the transformation of one form into another. Specifically, this development is in terms of a lack of awareness of others turning into an over-awareness of others, at adolescence. It is possible that that the bidirectional Δ RT pattern in the adolescence perspective taking results reflects this transformation – a period of change in the way social information about the self and others is processed, as well as an increase in efficiency. The results of the fMRI study on intention understanding further illustrate this view of adolescent cognitive development, but at the level of the brain. Additionally, action representation shows a refinement in the degree of ability, with age during adolescence. Taken together, the studies suggest that the refinement in representations of mental states, intentions and actions reported here is due to changing cognitive strategies and efficiency, paralleled by developments in neural strategies and in turn possibly underpinned by brain maturation in the relevant areas during adolescence.

7.10. Modelling social cognitive development during adolescence

The above sections have described how emotional perspective taking, intention understanding and action representation develop during adolescence, in terms of possible cognitive and neural strategies. This may be interpreted in terms of the Social Information Processing Network (SIPN) model (Nelson et al., 2005; see Introduction, Chapter 1). Like executive function abilities, social cognitive abilities are associated with components of the three nodes of the SIPN, including PFC, amygdala and STS. These social cognitive processes show development, while the neural substrates themselves show plasticity in terms of actual structure or changes in activity with age in the social cognitive tasks described in Chapter 1.

However, the SIPN is perhaps also limiting as it neglects the role of the PC. PC undergoes a developmental trajectory similar to that of PFC and is associated (particularly IPL) with processes related to social cognition, such as perspective taking in the motor, conceptual and emotional domains (Ruby & Decety, 2001; 2003; 2004), representation of one's own actions (Sirigu et al., 1995; 1996) and imitation of other people's actions (Decety et al., 2002; Jackson et al., 2006). Parietal development has already been linked to the improvement in abstract reasoning skills during adolescence (Luna et al., 2004b; Qin et al., 2004). Further investigations are required to determine how parietal development influences social cognitive development, and which regions are particularly involved.

New studies might continue to consider what *mechanisms* are directing social cognitive development. The SIPN proposes a "multi-step" route, in which neurally-based nodes process social stimuli in a sequential manner. Somewhere in this route, however, between detecting that a stimulus is animate and imbuing it with emotional significance, the brain must assign it to the correct agent. In other words, in the framework of the SIPN, an additional "agency node" linked to IPL might be involved in distinguishing whether the action is related to the self or to another before the limbic node would process approach or avoidance decisions and before the cognitive-regulatory node would perform higher level social processing. Indeed, as mentioned above, IPL seems to be involved in distinguishing between self and other, in terms of imagining how someone would think or feel (Ruby & Decety, 2003; 2004), making an action (Farrer &

Frith, 2002) or imagining making an action (Ruby & Decety, 2001). The current findings suggest that action understanding may be one mechanism that facilitates social understanding during adolescence.

A further speculation based on the results of the studies discussed is that puberty and adolescence represents a period of synaptic reorganisation and, as a consequence, the brain might be more sensitive to experiential input at this period of time in the realm of both executive function and social cognition. This sensitive period might be akin to sensitive periods of brain development evident in the early sensory system. Much like sound categorisation during language acquisition, experience with certain social cognitive skills might be much more difficult to incorporate into brain networks once they are established after adolescence. This notion is purely speculative and further research, preferably with input by multiple disciplines including educational researchers, cognitive scientists and neuroscientists, may shed light on this. The consequence might be that adolescence provides an extended period of learning, with a possible emphasis on the potential for social learning and development.

7.11. Implications for teenagers

Research into the cognitive implications of continued brain maturation beyond childhood may therefore be relevant to the social development and educational attainment of adolescents (although see Limitations and Future Directions). Further studies are necessary to reach a consensus about how axonal myelination and synaptic proliferation and pruning impact on social, emotional, linguistic, mathematical and creative development. In other words, which skills undergo perturbation, which undergo sensitive periods for enhancement and how does the quality of the environment interact with brain changes in the development of cognition? Longitudinal studies of the effect of early deprivation on the cognitive development of Romanian adoptees in the UK have begun to investigate this question (O'Connor & Rutter, 2000). Whether greater emphasis on social and emotional cognitive development would be beneficial during adolescence is unknown but research will provide insights into potential intervention schemes in secondary schools, for example, for remediation programs or anti-social behaviour.

Research in psychology and cognitive neuroscience can also contribute to the debate about juvenile crime, for instance on the current use of Anti-Social Behaviour Orders (ASBOs) in the UK. ASBOs are civil orders which can be imposed against anyone aged 10 or over who is deemed to have acted in a manner which 'causes harassment alarm or distress' to anyone, and which if breached become criminal offences. A dialogue between psychologists and parliamentarians would be useful to shape future legislative procedures concerning adolescent social behaviour. Current theoretical and philosophical underpinnings of criminal law are grounded in the principle of autonomy: individuals are regarded as rational autonomous human beings who can 'choose' their actions and are therefore held responsible by criminal law. This framework of the law is borrowed from philosophy rather than psychology. Drawing on recent experimental evidence from cellular, behavioural and brain imaging studies, neuroscientists and psychologists can evaluate the efficacy of ASBOs. Firstly, they can investigate the role of brain development in causing problem behaviour among adolescents. Secondly, given that the brain is still developing, psychologists can explore the long-term psychological effects of receiving an ASBO on the adolescent. Finally, neuroscience may offer insights into alternatives to current punitive methods. It may, for example, be worth allocating more resources to educational and rehabilitation programmes designed to take into account the natural developmental changes in adolescent psychology.

7.12. Limitations and future directions

Here, it is suggested that modifications to the tasks are made to enhance our understanding of the content of the development of form and efficiency of social cognitive processes. Both theoretical and empirical directions are suggested to further the investigations in this thesis and provide new perspectives on social cognitive development in adolescence and social cognition in autism and schizophrenia.

7.12.1. Paradigms for adolescent social cognition

Is it possible to know whether the task was in fact tapping participants' cognitive capacity for perspective taking? Can we know whether participants are likely to have used, for example, a simulation of their own actions to surmise the mental states of other agents in the 3PP? Rather, it is possible that when asked how a man would feel on finding a £5 note on the street, the mental state of hypothetical characters such as these

can be judged in an abstract, strategic manner, that does not involve reference to the self or application of self-knowledge to others, but instead the use of general semantic knowledge of 'what people feel when they find money unexpectedly', for example. An interesting modification to the task would be to use characters that have real meaning to all participants, following the Ruby & Decety (2003; 2004) fMRI studies of conceptual and emotional perspective taking. In the first of these tasks, 3PP and 1PP were contrasted by asking medical students what another medical student (3PP) versus a layperson (1PP) would think about medical questions. In the second task, how one's mother (3PP) would feel in certain situations was contrasted with how the participant (1PP) would feel. By bearing a certain familiar character in mind, these stimuli are perhaps more likely to tap this cognitive capacity and generate a starker contrast between the two perspective stances.

A more definitive idea of the content of the strategies that lead to these cognitive styles might be found from changes to the paradigm design. For example, modulating the difficulty of the questions beyond Open and Closed choice types, but in terms of familiarity of characters in the scenarios might enable us to elucidate more about how participants surmise 1PP and 3PP. The protagonists of the scenarios might in future be systematically varied by age, gender, familiar person, famous celebrity, and so on, to vary the 'psychological distance' between the participant and the character in the 3PP condition. If Δ RT became increasingly high with a direction of 3PP>1PP, as the protagonist became increasingly unfamiliar, this might suggest that a high 3PP RT reflects difficulty in identifying with the other character.

Once the meaning of longer (more difficult to process?) and shorter (easier to process?) RTs is ascertained, it would be interesting to investigate the role of selective inhibition in perspective taking. It has been proposed that we have a natural egocentric bias (e.g. Vorauer & Ross, 1999) such that we have a natural propensity to impose our own belief on our expectation of others' beliefs. One possibility is that in order to successfully surmise other people's beliefs and mental states, we are required to inhibit our own response. Inhibitory processes are thought to rely on PFC function and have been shown, through fMRI studies, to develop in parallel with PFC development during adolescence (e.g. Casey et al., 1997). A future investigation might interleave the current perspective taking task with a simple inhibition task to test the possible association

between executive function and social cognition, in particular. It is possible that development of inhibition of the 1PP might enable development of the ability to take the 3PP during the period of adolescence.

Individual differences in IQ have recently been shown to have a link to trajectories of brain development (Shaw et al., 2006). To supplement the fMRI data on the development of understanding intentional causality, it would be useful to determine how individual differences between subjects play a role in the activity in STS/MPFC. For example, questionnaires could be designed to provide a quantitative measure of self-consciousness, so that scores could be correlated with brain activity in different areas. It might be predicted that higher self-consciousness scores demonstrate greater activity in MPFC. The interpretation would be that greater MPFC activity would demonstrate higher incorporation of the mental states of others in the decision of what action follows one's own intention. It would be worth taking both self-report and parent-report questionnaire data to acquire a more accurate picture of self-consciousness.

A fuller account of adolescent social cognitive development requires a closer understanding of how higher cognitive processes interact with sex hormones and their influence the organisation of the brain's connectivity. It would be useful to investigate whether pubertal stage is linked to performance on the tasks described in this thesis. Further investigation of the influence of puberty on brain development and cognition would, however, benefit from objective and appropriate measures of pubertal development. Currently, if studies measure puberty at all, they tend to rely on self-ratings, parent reports or the judgements of teachers in schools. Investigators consistently report the difficulties met in ascertaining the level of pubertal development in adolescent, even using these methods. Not only do parents and teachers often consider them to be inappropriate to administer in schools, where much cognitive testing for such studies takes place, but they are also crude indices of pubertal status. It may be worth working with endocrinologists to investigate alternative reliable methods, such as using saliva swabs to test hormone levels. One study (McGivern et al., 2002) demonstrated using a match-to-sample task that cognitive efficiency is particularly slow around the age of puberty. The authors attributed this to exuberance of synapses in the required brain areas at puberty, although no measures of puberty were actually taken. It

would be worth validating this finding with further studies that are qualified with puberty measures.

7.12.2. Paradigms for clinical populations

A neurocontructivist approach to studying developmental disorders would emphasise caution on brain-based predictions about performance by typically and atypically developing adolescents that rest on the static neuropsychological model provided by adult lesion patients. This theoretical approach may be relevant to the interpretations made at the level of the brain for both the typical developmental studies and clinical studies presented here. fMRI studies, especially longitudinal designs for the developmental studies, would be more appropriate for making interpretations about development of brain mechanisms.

The caveats of neuropsychological lesion models and cross-sectional approaches can be illustrated for example in the case of the action representation study. Even if PC function is a constraint in development of action representation, development itself is likely to play a significant role in shaping the outcome by adolescence. In other words, development is a dynamic process, in which the progressive changes in processing as a function of time influence the final formation of cognitive functions (Bishop, 1997; Karmiloff-Smith, 1998). This makes it difficult to use adult studies to speculate on which brain areas might be driving a particular brain function at a given point in development. It has been suggested that cognitive modules are not innately specified, but rather, that developmental processes begin with domain-relevant modules, which are initially usable, but less efficient, for more than one function and become refined over time until they are particularly efficient for a specific function (Karmiloff-Smith, 1998). Imaging the developing brain using fMRI during motor imagery tasks would provide a better picture of neural networks that are activated to a lesser or greater extent during adolescence. Depending on the synchrony of brain development, different regions might be more or less involved at different time points of development. For example, PFC is known to be involved in working memory or holding in mind actions (Gilbert et al., 2005) and might be more involved in motor imagery in late adolescence, whereas the PC might be implicated more in early adolescence. This hypothesis is based on the relative rates of maturation of these brain areas and the fact that PFC function may also be relevant to this task. This may also be tied to the possibilities that lower

level developmental events in the brain such as dendritic arborisation, synaptogenesis and synaptic pruning, play different roles with greater of lesser influence on cognition at different times.

It could be particularly problematic to predict that functions such as action representation will be disrupted in ASD in the same way as in adult parietal lesion patients simply because of atypical development of parietal morphology in ASD. It would be a fallacy to conclude that no difference in the E-I correlation between ASD and TD adolescents suggests no developmental differences in the action representation system in ASD or to assume this reflects that parietal areas involved in action representation are 'intact' in ASD. This would be relying on a static picture provided by adult imaging and lesion studies which does not incorporate the dynamic nature of development. This dissociation logic is unlikely to be applicable to development. One interpretation for the lack of difference in motor imagery performance between groups could be that ASD adolescents use a different cognitive process to arrive at approximately the same level of performance as TD adolescents. This may be because of the reorganisation of the brain that takes place in an atypical manner in ASD, but it is important to note that this atypical development is also dynamic. In other words, reorganisation which might occur in response to abnormal parietal and cerebellar morphology in early infancy in ASD would have knock-on effects on the organisation and functional roles and specificity of other brain areas.

The study of perspective taking in affective and schizophrenic patients was limited by two fundamental constraints. Firstly, there was often a lack of consensus between clinicians as to the diagnosis of patients. For this reason, delusions were considered on a continuum for part of the analysis and all patients placed in one group. However, the measurement of particular symptoms was also problematic. The PANSS involves determining the level of delusional and hallucinatory behaviour, which in turn requires consensus on a qualitative definition of delusions and hallucinations. While DSM IV provides diagnostic definitions, these also proved to be subject to different interpretations that were not always confirmed by different clinicians. Almost every clinical patient involved in the study had a context of emotional distress surrounding their case. Although each case was individually discussed to contextualise the content what was potentially considered a delusion or hallucination, there was often

disagreement as to whether the description in each case conformed to diagnostic criteria (cf. Bell et al., 2006 for a brief discussion of assumptions of criteria for the diagnosis of delusional behaviour). Secondly, the results of the study may have been confounded by the different types of medication taken by each patient. Each patient had a separate constellation of symptoms, for which they were prescribed particular types and varieties of medication. It was not possible to test the patients free of medication, or to match the medication types between patient groups, and thus, results were contaminated by possible side effects such as varying degrees of slowing of reaction speed or adverse effects on memory.

7.12.3. Viewing the brain as necessary but not sufficient in an explanatory account of adolescent social cognitive development

This thesis has investigated and interpreted development of social cognitive skills within a cognitive neuroscience framework that assumes behaviour is underpinned by neurally based cognitive mechanisms. The assumption has therefore been that the development of the organisation of the brain gives rise to the functional refinements in cognitive mechanisms. The importance of individual differences has already been discussed above, where the necessity of studying how differences in levels of self-consciousness and introversion/extroversion might influence social cognitive processing was emphasised. While it was suggested above that knowledge of the developing brain must be taken into account for social and educational policy, a cautionary note about this is also important. Adolescence is inextricably bound up with major socio-cultural influences, including the change of familial and societal expectations, the changing school environments involving qualitatively different peer and adult interactions as well as influences from media about the role of adolescents, which itself is subject to constant flux. There is therefore a complex reciprocal relationship and interaction between biological development and the social environment, both of which must be considered as dynamic in nature. Of course, biology places several constraints, at the level of genetics and the brain, on cognitive development. These are also most likely pre-specified through evolution. However, the findings presented here are best viewed within a theoretical framework that considers protracted neocortical development, itself, as evolutionarily specified, thus placing more emphasis on the adaptation of the human brain for extended learning and flexibility during the socially and culturally demanding period of adolescence. It is also noteworthy that the hypotheses and interpretations

discussed here about adolescence are based on the Western notion of 'adolescence' and its associated social repertoires. Different cultural practices and socio-economic contexts place different sets of constraints on behavioural development during adolescence. For example, 'adolescence' is a Western construct that is not necessarily relevant in many non-Western cultures in which the transition from childhood to adulthood is immediate due to different family duties and physical labour needs and contrasting values placed on the development of the individual versus the collective (see Timimi & Maitra, 2005 for a critique of mainstream medical models of adolescent psychology and psychiatry). As such, there is often less emphasis on prolonged social development in non-Western cultures. It was suggested above that the adolescent brain has evolved to undergo an extended period of plasticity, perhaps in order to enhance socio-cultural learning at a period of changing roles. While brain development may be universal, the cognitive consequences may be entirely different given the two-way interaction between the brain and the socio-cultural environment.

7.13. Overall conclusions

This thesis has provided novel findings showing development of social cognitive skills, in terms of cognitive and neural mechanisms, during adolescence. Why should social understanding develop at all during adolescence? Adolescents must be equipped with the means to negotiate contact in complex social institutions, including the family and the school environment. The development of social understanding perhaps endows adolescents with the skills and motivation to engage collaboratively and collectively in new social contexts at adolescence. The development of the adolescent brain and social cognitive mechanisms may facilitate this period of refinement of cultural cognition (Tomasello et al., 2005).

In this thesis, a developmental cognitive neuroscience framework has been used, but a richer account of changes in adolescent learning, strategic and social behaviour requires a multidisciplinary approach that recognises the complex interactions between genetics, brain structure, physiology and chemistry and the socio-cultural environment. Studying the development of adolescent cognition using complimentary in vivo methods that exploit the advantages of a variety of behavioural and neuroimaging techniques, within a theoretical framework that regards motor, affective, social and perceptual functions as intertwined, promises to further inform our understanding of typical and atypical adolescent behaviour.

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APPENDICES

APPENDIX 2

PERSPECTIVE TAKING PARADIGM

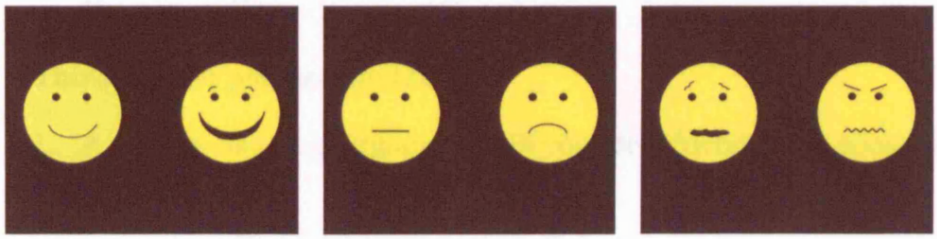
Every question screen (with a written scenario) was followed by an answer screen (a choice of two emotional faces), as follows.

There were two choice types: Open and Closed
The Open condition presented two equally appropriate answers,, while the Closed condition presented one correct and one incorrect answer to the preceding question.

Example of question stimulus:

1PP	3PP
You get told off for talking during a lesson. **How do you feel?**	**A student gets told off for talking during a lesson.** **How does she feel?**

Each answer screen presented two of the following emotion faces:



Happy Very happy Neutral Sad Afraid Angry

RT to choose a face thought to best answer the question was recorded

EXAMPLES OF QUESTIONS FROM PERSPECTIVE TAKING TASK FOR PRE-ADOLESCENTS, ADOLESCENTS AND ADULTS

(Written emotion choices were depicted as cartoon emotion faces as illustrated on previous page)

First-person perspective (1PP)

1. You have had a big argument with your best friend. How do you feel?

   Neutral or Sad *[Open]*

2. You get told off for talking during a lesson at school. How do you feel?

   Very happy or Afraid *[Closed]*

3. You are told that your maths test has been cancelled. How do you feel?

   Very happy or neutral *[Open]*

4. You get autographs from the stars at the opening of a film. How do you feel?

   Very happy or Angry *[Closed]*

5. You find a five-pound note while walking along. How do you feel?

   Neutral or Happy *[Open]*

Third-person perspective (3PP)

1. A girl has had a big argument with your best friend. How does she feel?

   Neutral or Sad *[Open]*

2. A boy gets told off for talking during a lesson at school. How does he feel?

   Very happy or Afraid *[Closed]*

3. A boy is told that his maths test has been cancelled. How does he feel?

   Very happy or neutral *[Open]*

4. A man gets autographs from the stars at the opening of a film. How does he feel?

   Very happy or Angry *[Closed]*

5. A woman finds a five-pound note while walking along. How does she feel?

   Neutral or Happy *[Open]*

APPENDIX 3A

EXAMPLES OF QUESTIONS FROM PERSPECTIVE TAKING TASK FOR PSYCHIATRIC ADULT PATIENTS IN VERSAILLES, FRANCE

First-person perspective (1PP)

1. Un admirateur secret vous envoie un bouquet de fleurs. Comment vous sentez- vous?
   (A secret admirer sends you a bouquet of flowers. How do you feel?)

   Happy or Very happy *[Open]*

2. Votre ami vous offre une caisse de vin pour vous remercier de votre aide. Comment vous sentez-vous?
   (Your friend gives you a case of wine to thank you for some help. How do you feel?)

   Happy or Afraid *[Closed]*

3. Vous réalisez que vous avez perdu votre nouvelle montre à une soirée. Comment vous sentez-vous?
   (You realise you have lost your new watch at a party. How do you feel?)

   Neutral or Sad *[Open]*

4. Vous avez eu une grosse dispute avec votre collègue. Comment vous sentez-vous?
   (You realise you have lost your new watch at a party. How do you feel?)

   Angry or Happy *[Closed]*

5. Le parti politique pour lequel vous avez voté perd les élections finales. Comment vous sentez-vous?
   (The political party you vote for loses in the general election. How do you feel?)

   Angry or Sad *[Open]*

Third-person perspective (1PP)

1. Un admirateur secret envoie un bouquet de fleurs à une femme. Comment se sent-elle?
   (A secret admirer sends a woman a bouquet of flowers. How does she feel?)

   Happy or Very happy *[Open]*

2. Un homme offre une caisse de vin à son amie pour la remercier de son aide. Comment se sent-elle ?
   (A man gives his friend a case of wine to thank her for some help. How does she feel?)

Happy or Afraid *[Closed]*

3. Un homme réalise qu'il a perdu sa nouvelle montre à une soirée. Comment se sent-il ?
   (A man realises he has lost his new watch at a party. How does he feel?)

   Neutral or Sad *[Open]*

4. Une femme a eu une grosse dispute avec son collègue. Comment se sent-elle ?
   (A woman has had a big argument with her colleague. How does she feel?)

   Angry or Happy *[Closed]*

5. Le parti politique pour lequel l'homme a voté perd les élections finales. Comment se sent-il ?
   (A man finds out that the political party he voted for loses in the general election. How does he feel?)

   Angry or Sad *[Open]*

APPENDIX 3B

POSITIVE AND NEGATIVE SYNDROMES SCALE
PANSS

NOM PRENOM

SEXE AGE DATE

EXAMINATEUR

CONSIGNES

Entourer la cotation appropriée a chaque dimension, a la Suite de l'entretien clinique spécifique. Se reporter au Manuel de Cotation pour la définition des items, la description des différents degrés et la procédure de cotation.

1 = Absence; 2 = Minime; 3= Légère; 4= Moyenne; 5 = Mod. Sévère; 6 = Sévère; 7=Extrême

ECHELLE POSITIVE

P1 Idées délirantes
P2 Désorganisation conceptuelle
P3 Activité hallucinatoire
P4 Excitation
P5 Idées de grandeur
P6 Méfiance/Persécution
P7 Hostilité

ECHELLE NEGATIVE

N1 Amusement de l'expression des émotions
N2 Retrait affectif
N3 Mauvais contact
N4 Repli social passif/apathique
N5 Difficultés d'abstraction
N6 Absence de spontanéité et de fluidité dans la conversation
N7 Pensée stéréotypé

ECHELLE PSYCHOPATHOLOGIQUE GENERALE

G1 Préoccupations somatiques
G2 Anxiété
G3 Sentiments de culpabilité
G4 Tension
G5 Maniérisme et troubles de la posture

G6 Dépression
G7 Ralentissement psychomoteur
G8 Manque de coopération
G9 Contenu inhabituel de la pensée
G10 Désorientation
G11 Manque d'attention
G12 Manque de jugement et de prise de conscience de la maladie
G13 Trouble de la volition
G14 Mauvais contrôle pulsionnel
G15 Préoccupation excessive de soi (tendances autistiques)
G16 Evitement social actif

TRANSLATION OF THE PANSS SCALE FROM FRENCH. EACH ITEM WAS SCALED FROM 1-7 (1 = ABSENCE; 7 = HIGHEST LEVEL)

POSITIVE SCALE

P1 Delusional ideation
P2 Conceptual disorganisation
P3 Hallucinations
P4 Agitation
P5 Delusions of grandeur
P6. Delusions of persecution
P7. Hostility

NEGATIVE SCALE

N1 Emotional bluntness
N2 Affective withdrawal
N3 Poor contact
N4 Social withdrawal
N5 Difficulties in contextualising
N6 Absence of spontaneity and fluidity of conversation
N7 Stereotyped thoughts

GENERAL PSYCHOPATHOLOGICAL SCALE

G1 Somatic anxiety
G2 Anxiety
G3 Feelings of guilt
G4 Nervous tension
G5 Problems with mannerism and posture
G6 Depression
G7 Psychomotor slowing
G8 Lack of co-operation
G9 Unusual thought content
G10 Disorientation
G11 Lack of focus
G12 Lack of judgement and consciousness of illness
G13 Disorders of volition
G14 Poor impulse control
G15 Excessive preoccupation with the self (autistic tendencies)
G16 Social avoidance behaviours

APPENDIX 4

EXAMPLES OF QUESTIONS FROM INTENTION UNDERSTANDING FMRI TASK

Intentional Causality (IC)

1. You want to sunbathe but don't want to get sunburnt.

   Do you put on sun screen?

2. You want to find out what is on at the cinema.

   Do you look in the newspaper?

3. You want to be healthy and are choosing lunch.

   Do you share the lunch?

4. Your friend phones and invites you to go to the park.

   Do you buy a new book?

5. You can't find your homework and are late for school.

   Do you feed the pigeons?

Physical Causality (PC)

1. It is summer and the rays of sunshine are very strong.

   Does it cause the ground to warm up?

2. It is stormy weather and the sea is very rough.

   Does it cause large waves to form?

3. It is very windy and there is a gale outside.

   Does it cause the birds to sing?

4. The flowers in the garden have not been watered.

   Does it cause the door to swing open?

5. The kettle of water is hot and about to boil.

   Does it cause the sun to shine brightly?

APPENDIX 5

PRAXIS IMAGERY QUESTIONNAIRE
(adapted from Ochipa et al., 1997 and Wilson et al., 2001)

A1. Kinaesthetic subscale

1. Imagine that you are writing your name with a pencil. Which joint moves more, your wrist or your finger joints?
2. Imagine you are cleaning your teeth. Which moves more, your wrist or finger joints?
3. Imagine you are eating with a spoon. Which joint moves more, your finger or your wrist?
4. Imagine you are flicking on a light switch. Which moves more, your finger joint or your elbow joint?
5. Imagine you are zipping up a jacket. Which moves more, your elbow or shoulder joints?
6. Imagine you are drinking out of a glass. Which moves more, your wrist or your shoulder joints?
7. Imagine you are using a pencil sharpener. Which joint moves more, your wrist or elbow joints?

A2. Position subscale

1. Imagine you are writing your name with a pencil. Which is closer to the paper, your index finger or your pinky?
2. Imagine you are cleaning your teeth. Is your arm bent or straight?
3. Imagine you are eating with a spoon. Is your hand open or closed?
4. Imagine you are flicking on a light switch. Is your palm facing towards your body or away from you?
5. Imagine you are zipping up a jacket. Is your palm facing towards your body or away from you?
6. Imagine you are drinking out of a glass. Which is closer to your body, your fingers or your thumb?
7. Imagine you are sharpening a pencil. Are your fingers bent or straight?

A3. Action subscale

1. Imagine you are writing your name with your right hand. Does your hand move towards or away from your body?
2. Imagine you are cleaning your teeth. Do you move your toothbrush around you mouth, or your mouth around your toothbrush?
3. Imagine you are eating soup with a spoon. Do you move the spoon straight towards your body or in a circle?
4. Imagine you are flicking on a light switch. Does your finger move up and down, or to the side?
5. Imagine you are zipping up a jacket. Does your hand move towards your neck or shoulder?

6. Imagine you are drinking out of a glass. Does the bottom of the glass move towards the floor or the roof?
7. Imagine you are sharpening a pencil. Does your hand move in a circle, or up and down?

A4. Object subscale

1. Which is wider, the eraser at the end of a pencil or the point?
2. Is the end of the toothbrush you put in your mouth usually rectangular or round?
3. Is a spoon bigger where you hold it, or where you put it in your mouth?
4. Which is bigger, a light switch or a door handle?
5. Does a clothes zip have teeth on both sides before being done up? Yes/No
6. Is a drinking glass usually wider at the top of the glass or at the base?
7. When you put a pencil in a pencil sharpener, is the hole square or round?